

THE BOTANICAL GAZETTE

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No. 1, July 16; No. 2, August 21; No. 3, September 25; No. 4, October 24; No. 5, November 20; No. 6, December 22.

ERRATA

- P. 41, line 6 from below, for genera read families.
 P. 77, line 12, for *diem* read *idem*.
 P. 133, Fig. 3, legend, for Nupha read Nuphar.
 P. 156, line 1, for Intercellular read Intracellular.
 P. 156, line 1 from below, for 487 read 187.
 P. 171, line 12 from below, for has read is.
 P. 175, line 2, for Tschapolwitsch read Tschaplowitz.

- Pp. 214-215. Interchange legends of plates IV and V.
P. 215, under "Explanation of Plates" interchange the plate numbers IV and V.
P. 239, line 23, for *Argrostis* read *Agrostis*.
P. 273, line 9, for Curtiss read Curtis.
P. 275, line 5, for Barenetzky read Baranetzky.
P. 347, line 13 from below, for (*figs. 29, 30*) read (**29, 30**).
P. 347, line 8 from below, for (*fig. 35*) read (*fig. 37*).
P. 348, line 1, for (*fig. 40*) read (*fig. 35*).
P. 354, line 5 from below, for FIG. 35 read FIG. 37.
P. 354, line 3 from below, for FIGS. 36-39 read FIGS. 36, 38, 39.
P. 354, last line, for FIG. 40 read FIG. 35.
P. 364, line 5 from below, **Abronia cheradophila** should read **ABRONIA AMMO-**
PHILA Greene, Pittonia 4:226.
P. 370, line 11, for **Cartaegus** read **Crataegus**.
P. 420, insert as sub-title **SCLEROSPORA GRAMINICOLAE** (Sacc.) Schroet.



BOTANICAL GAZETTE

JULY, 1902

THE UREDINEÆ OCCURRING UPON PHRAGMITES,
SPARTINA, AND ARUNDINARIA IN AMERICA.¹

J. C. ARTHUR.

(WITH FOUR FIGURES)

UPON the several species of Phragmites, Spartina, and Arundinaria there occur in America one species of Uromyces and six species of Puccinia. There has never existed material confusion regarding the Uromyces species, except to divide it into two upon geographical grounds; but the Puccinia species have been so much confused and misunderstood that one may say with much truth that, whenever a correct determination has been made, it has been due more to good fortune than to clear insight. The most common disposition of these six species has been to list them indiscriminately under *P. Phragmitis* (Schum.) Körn., or possibly under *P. arundinacea* Hedw. or DC., or occasionally under *P. Arundinariæ* Schw. In 1876 Körnicke² showed that in Europe two species of Puccinia occur upon Phragmites that are morphologically distinguishable, which he diagnosed under the names *P. Phragmitis* and *P. Magnusiana*. The first of these species appears to be cosmopolitan and occurs in America, but not the second one. This second species is represented by a closely related one, however, which, together with the other four species of Puccinia and one of Uromyces described in this

¹Presented by title at the Columbus meeting of the Botanical Society of America, Ag 1899.

²Hedwigia 15: 178. 1876.

paper, appears to be exclusively American. Several European species now known to occur upon *Phragmites* have not yet been found in America.

The writer's attention was first called to the confusion in the American species when studying the uredospores upon *Spartina*, preparatory to undertaking cultures. The results of subsequent study are now presented in systematic order, and with sufficient fullness, it is believed, to permit of the ready identification of material.

In this paper, whenever actual specimens are cited, the kind and abundance of the spores present are indicated by the cipher and Roman numerals: O. I. II. III. If the spore receptacles are well formed and fairly abundant, large (capital) type is used; and if the spores are few and subordinate, small (lower-case) type is used. Thus, II, iii, indicates that well-formed uredosori are present, but that the teleutosori are comparatively few, or that what teleutospores are present are borne in the uredosori.

Grateful acknowledgment is made to a number of mycologists for the loan of specimens. Professor T. J. Burrill of the University of Illinois, Professor L. H. Pammel of the Iowa State College, Professor W. G. Farlow of Harvard University, Professor L. R. Jones of the University of Vermont, Professor F. S. Earle of the Alabama Polytechnic Institute, and the custodians of the Philadelphia Academy of Sciences and the New York Botanical Gardens, placed a portion of the herbaria under their charge at my disposal; while the following botanists either loaned specimens from their herbaria or gathered material from the field for my use: Messrs. H. L. Bolley, R. I. Cratty, E. W. D. Holway, G. W. Carver, H. H. Hume, J. J. Davis, E. Bartholomew, S. M. Tracy, T. H. MacBride, P. H. Rolfs, L. M. Underwood, and C. E. Bessey. I am furthermore especially indebted to Mr. A. B. Seymour for the generous loan of a part of his herbarium, which proved remarkably rich in collections representing nearly all the species covered by this paper.

All figures accompanying this paper are drawn with camera

lucida to a uniform scale of 470 diameters, and all are in vertical section, excepting three uredospores which are in transverse section (see explanation of *figs. 3 and 4*). The pedicels are as carefully drawn as the rest of the spore.

I. *UROMYCES ACUMINATUS* Arth. 1883, May. Bull. Minn. Acad. Sci. 2:35.

SYN.: 1883, July. *Uromyces Spartina* Farl. Proc. Amer. Acad. Sci. 18: 77.

EXSICC.: Ellis, N. Amer. Fungi, 239^{III}, 1443^{III}.

Sydow, Uredineen, 251^{III}.

Seymour and Earle, Econ. Fungi, 67^{III}, 68^{III}, 546^{III}.

O. I. Spermogonia and aecidia unknown.

II. III. Sori epiphyllous, intercostal, linear, soon naked, ruptured epidermis conspicuous. II. Uredosori yellowish, inconspicuous; uredospores globose or broadly elliptical, large, 22–35 μ in diameter, average 30 μ , wall golden yellow, thick while immature, becoming thin, echinulate with low, stout points, pores 5 to 8, scattered. III. Teleutosori blackish-brown, sunken between the nerves or protruding; teleutospores dark brown, obovate or oblong-clavate, 15–22 by 25–40 μ , apex darker, acuminate or obtuse, or with two or more projections, much thickened, 8–12 μ , base narrowed, pedicel colored, firm, once to thrice length of the spore, often shorter.

From Massachusetts to Illinois and Nebraska and northward; especially abundant in the upper Mississippi valley. On leaves of the several species of *Spartina*; the uredospores in July, soon followed by the teleutospores, which persist through the winter and germinate the following spring. Specimens have been examined as follows:

On *Spartina cynosuroides* (L.) Willd. 1881, III, Illinois (1326, *A. B. Seymour*); Sept. 1882, III, Ft. Dodge, Iowa (type of *Urom. acuminatus* Arth., *J. C. Arthur*); Nov. 1882, III, Decorah, Iowa (*E. W. D. Holway*); Dec. 1882, III, Spirit lake, Iowa (*J. C. Arthur*); July 1883, II, Spirit lake, Iowa (*J. C. Arthur*); Sept. 1883, III, Decorah, Iowa (Ellis, N. Am. Fungi, 1443, *E. W. D. Holway*); Dec. 1883, III, Spirit lake, Iowa (*J. C. Arthur*); Aug. 1884, III, Bismarck, N. D. (Journey to Washington Territory, 297, 298, *A. B. Seymour*); Aug. 1884, III, Valley city, N. D. (Journey to Washington

Territory, 299, *A. B. Seymour*); Sept. 1884, III, Decorah, Iowa (*E. W. D. Holway*); Oct. 1885, III, Decorah, Iowa (Sydow's Uredineen, 251, *E. W. D. Holway*); July 1886, II. iii, Emmet co., Iowa (*R. I. Cratty*); Aug. 1886, III, Emmet co., Iowa (524, *R. I. Cratty*); Oct. 1888, III, Racine, Wis. (*J. J. Davis*); Aug. 1898, II. iii, Spirit lake, Iowa (*J. C. Arthur*); April 1899, III, Ames, Iowa (Cryptogams: Plants of Iowa distributed by the Iowa State College, 47, *H. H. Hume*); July 1899, II. III, Fargo, N. D. (*H. L. Bolley*); Aug. 1899, ii. III, Long Pine, Neb. (*J. M. Bates*); Oct. 1901, III, Fargo, N. D. (*H. L. Bolley*); no date, ii. III, Canada (1193, *C. G. Pringle*).

On *Spartina gracilis* Trin. Sept. 1884, III, Medora, N. D. (Journey to Washington Territory, *A. B. Seymour*); July 1901, II. III, Gleichen, Alberta, Can. (*E. W. D. Holway*).

On *Spartina glabra* Muhl. No date, II. III, Woods Hole, Mass. (Ellis' N. Amer. Fungi, 239, type collection of *Urom. Spartinae* Farl., *W. G. Farlow*); Oct. 1889, III, Cambridge, Mass. (Seymour and Earle's Economic Fungi, 68, *A. B. Seymour*).

On *Spartina patens* (Ait.) Muhl. Oct. 1889, III, Cambridge, Mass. (Seymour and Earle's Econ. Fungi, 67, *A. B. Seymour*); Sept. 1899, ii, III, Portland, Me. (*J. C. Arthur*).

The species apparently finds its greatest development, judging by the abundance of the teleutosporic stage, in the prairie region of the upper Mississippi valley and northward, although, judging by the fullness and prominence of the sori and plumpness of the spores, it flourishes best along the northern Atlantic shores. No one has yet been able to suggest the probable aecidial stage, which should be known before pronouncing upon the conditions best suited to the species. Dr. W. G. Farlow,³ in notes on the first collection made at the seashore, mentions his failure to find any aecidium in the vicinity that could reasonably be associated with it, and several times in northern Iowa, where the species is especially abundant, the writer has made careful search for a related aecidium, but wholly in vain.

The teleutospores of this species, as well as their sori, are quite variable (*fig. 1, a to e*). Collections made from salt marshes near the sea, which have heretofore been called *Urom. Spartinae* Farl., have the sori prominent, and the teleutospores with more rounded apices, and, in general, a deeper-colored, more luxuriant appearance (*fig. 1, c*). This richer development

³ Proc. Amer. Acad. Sci. 18: 77.

also extends somewhat to the uredospores, which generally are larger and have thicker walls. But these characteristics are not wholly absent from inland specimens. They are quite as well shown in both sori and spores in two collections from Alberta and North Dakota in the northwest, both on *Spartina gracilis* (fig. 1, e), and also, so far as the spores are concerned, in a specimen from Nebraska (Bates, Aug. 1899) and one from Wisconsin (Davis, Oct. 1888), both on *S. cynosuroides* (fig. 1, b and d). The latter specimen is in the herbarium of Mr. A. B. Seymour,

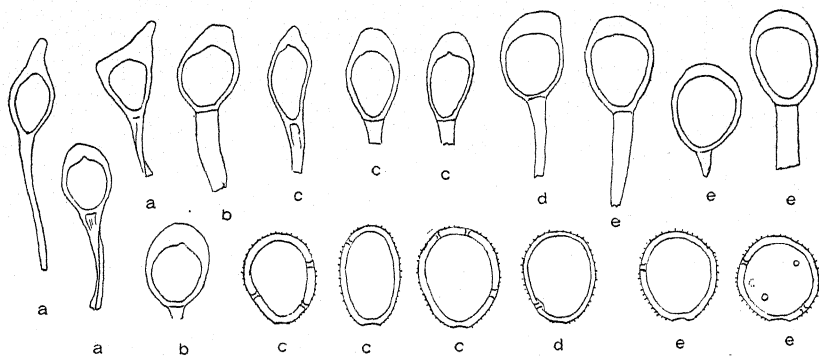


FIG. 1.—*U. acuminatus*: a, three teleutospores showing size and diverse forms common on the western prairies, on *Spartina cynosuroides* from Iowa; b, two teleutospores on same host from Wisconsin (Davis, 1888); c, three uredospores and three teleutospores of the typical *U. Spartinae* Farl. common along the seashore, on *Spartina glabra* from Woods Hole, Mass.; d, one uredospore and one teleutospore on *Spartina cynosuroides* from Nebraska (Bates, Aug. 1899); e, two uredospores and three teleutospores on *Spartina gracilis* from Alberta (Holway, 1901).

and is accompanied by the following note, probably made by the collector: "Has the large, blunt-warted uredospores of *Urom. Spartinae*, but hardly the long and broad pedicels of the teleutospores, nor the large, elongated sori; it has darker and more rounded teleutospores than *Urom. acuminatus*." This note brings out clearly the distinctions that have been maintained between the two forms.

Of the variability of the teleutospores of the inland form Burrill⁴ makes the following observations (fig. 1, a): "Among

⁴Parasitic fungi of Illinois, Bull. Ill. Lab. Nat. Hist. 2:169.

the Uromycetes inhabiting grasses this is readily distinguished by the irregular and peculiar shape of the teleutospores; while some are no longer than wide, many are oblong or nearly lanceolate, while the apex has a multitude of forms; sometimes straight, sometimes acutely acuminate, often turned sidewise, beak-like, not seldom double, and occasionally suggesting the appendages at the apex of the teleutospores of *Puccinia coronata*." The paler, more slender, and poorly nourished teleutospores of the inland form are associated with the smaller sori, which are sunken and compressed between the stout nerves of the leaves.

If there are specific differences between the seashore and inland forms of this rust, they can only be established with certainty by cultures. Morphological characters derived from the uredo and teleuto stages show no differences that are not accounted for by ecological conditions.

The species was first recorded by Farlow⁵ in 1878 under the name *Urom. Junci*. The following year the same collection was distributed in Ellis' *North Amer. Fungi*, No. 239, under the name *Urom. Junci* var. *Spartinæ*, but without description. Later study resulted in raising the form to specific rank, as given in the synonymy above.

2. PUCCINIA FRAXINATA (Lk.), nom. nov.

SYN.: 1822. *Aecidium Fraxini* Schw. Schrift. d. nat. Ges. zu Leipzig 1:66.

1825. *Caeoma Fraxinatum* Link. Linné Sp. Pl. 6²:62.

1834. *Caeoma (Roestelia) Fraxinites* Schw. Trans. Amer. Phil. Soc.

4:294.

1890. *Uredo peridermiospora* E. & T. Jour. Myc. 6:77.

1896. *Puccinia sparganioides* E & B. Erythea 4:2.

1899. *Puccinia peridermiospora* Arth. Science 10:565.

EXSICC.: Ellis and Everhart, N. Amer. Fungi, 1851^{III}, 3475^{III}.

Ellis and Everhart, Fungi Columb., 1288^{III}.

Carleton, Ured. Amer., 33^I.

Sydow, Uredineen, 262^{III}, and 1167^{III}.

O. I. *Spermogonia* epiphyllous, yellow, inconspicuous;

⁵ Bull. Bussey Inst. 2:225 and 243.

spermatia obovate or oblong, about 3 by 5 μ . Aecidia hypophyllous, or on petioles and fruit, in dense rounded groups, usually on swollen and discolored spots; peridia cylindrical, often elongated, margin lacerated; aecidiospores obovate or elliptical, 22-26 by 33-37 μ , contents orange when fresh, becoming faintly yellow when old, wall colorless, thin at the sides but greatly thickened at the obtuse apex, tuberculate.

II. III. Sori hypophyllous, amphigenous on some hosts, supercostal, very prominent, large, oblong, elongated on sheaths and culms, ruptured epidermis attached in shreds or disappearing. II. Uredosori pulverulent, at first bright orange, becoming yellowish and indistinct; uredospores obovate or elliptical, 22-30 by 33-44 μ , contents orange when fresh, becoming faintly yellow when old, wall colorless, thin at the sides but greatly thickened at the rounded apex, prominently tuberculate, pores obscure. III. Teleutosori pulvinate, blackish-brown; teleutospores elliptical or oblong, 16-22 by 35-62 μ , dark brown, slightly constricted at the septum, apex obtuse, thickened; pedicel firm, slender, tinted, once to twice the length of the spore

Common throughout the United States and Canada east of the Rocky mountains. On leaves, petioles, and fruiting inflorescence of the various species of *Fraxinus* and *Spartina*; spermogonia and aecidia May to July, uredo in July and August, followed shortly by the teleutospores, which persist through the winter and germinate the next spring. Specimens have been examined as follows:

On *Fraxinus lanceolata* Borck. (*F. viride* Michx.) May 1871, O. I., Ames, Iowa (*J. C. Arthur*); July 1883, O. I., Spirit lake, Iowa (*J. C. Arthur*); 1886, I., Washington, D. C. (collector not recorded); June 1892, O. I., Rockport, Kan. (*E. Bartholomew*); June 1892, I., Manhattan, Kan. (Carleton's Ured. Amer., 33, *M. A. Carleton*); Aug. 1898, I., Heron lake, Minn. (*J. C. Arthur*); May and June 1899, O. I., Lafayette, Ind. (grown from teleutospores on *Spartina* by the writer, *J. C. Arthur*); June 1899, I., Ames, Iowa (*H. H. Hume*); July 1899, I., Spirit lake, Iowa (*J. C. Arthur*); Aug. 1899, I., South Hero, Vt. (*L. R. Jones*); June 1900, O. I., Spirit lake, Iowa (*J. C. Arthur*); July 1901, I., Crow agency, Mont. (237, *J. W. Blankinship*).

On *Fraxinus Americana* L. June 1889, O. I, Iowa city, Iowa (*Mrs. M. F. L. Fitzpatrick*).

On *Fraxinus Pennsylvanica* Marsh. (*F. pubescens* Lam.). June 1899, O. I, Long pine, Neb. (*J. M. Bates*); Aug. 1899, I, South Hero, Vt. (*L. R. Jones*).

On *Fraxinus nigra* Marsh. (*F. sambucifolia* Lam.). July 1884, o. I, La Crosse, Wis. (*L. H. Pammel*).

On *Fraxinus* sp. indet. No date, o. i, Bethlehem, Pa. (Type of *Æcid. Fraxini* Schw., *L. von Schweinitz*).

On *Spartina cynosuroides* (L.) Willd. Aug. 1882, III, Charles city, Iowa (*J. C. Arthur*); Oct. 1882, III, Ames, Iowa (*J. C. Arthur*); Oct. 1882, III, Urbana, Ill. (6335, *A. B. Seymour*); Oct. 1882, III, Ames, Iowa (*J. C. Arthur*); Nov. 1882, III, Decorah, Iowa (*E. W. D. Holway*); Dec. 1883, III, Spirit lake, Iowa (*J. C. Arthur*); Aug. 1884, III, Bismarck, N. D. (Jour. to Wash. Terr., *A. B. Seymour*); Oct. 1885, III, Decorah, Iowa (*E. W. D. Holway*); Oct. 1885, III, Urbana, Ill. (*M. B. Waite*); Oct. 1889, III, Decorah, Iowa (Sydow's Ured., 262, *E. W. D. Holway*); Oct. 1890, III, Racine, Wis. (*J. J. Davis*); Oct. 1892, III, Brookings, S. D. (*David Grif-fiths*); Oct. 1892, III, Ames, Iowa (*G. W. Carver*); Aug. 1895, ii. III, Rooks co., Kan. (Type of *Puc. sparganioides* E. & E., 1908, *E. Bartholomew*); Aug. 1897, III, Rooks co., Kan. (Ellis and Everhart's Fungi Columb., 1288, *E. Bartholomew*); Oct. 1897, III, Rooks co., Kansas (*E. Bartholomew*); July and Aug. 1898, II. III, Spirit lake, Iowa (*J. C. Arthur*); Oct. 1898, III, Alburgh, Vt. (*W. A. Orton*); April 1899, III, Lincoln, Neb. (in part used by the writer for successful cultures on *Fraxinus*, *W. T. Horne*); May 1899, III, Fargo, N. D. (*H. L. Bolley*); May 1899, III, Ames, Iowa (in part used by the writer for successful cultures on *Fraxinus*, *H. H. Hume*); July 1899, II. III, Fargo, N. D. (*H. L. Bolley*); Aug. 1899, II. iii, Ames, Iowa (*H. H. Hume*); Aug. 1899, III, South Hero, Vt. (*L. R. Jones*); Aug. 1899, III, O'Neill, Neb. (*J. M. Bates*); Oct. 1900, III, Orono, Me. (*R. L. Ricker*); No date, III, Stillwater, Okla. (*E. E. Bogue*); No date, III, Ft. Dodge, Iowa (*J. C. Arthur*).

On *Spartina glabra* Muhl. Sept. 1889, II, Ocean springs, Miss. (type of *Uredo peridermiospora* E. & T., *S. M. Tracy*).

On *Spartina polystachya* (Michx.) Willd. Oct. 1886, III, Point a la Hache, La. (Ellis and Everhart's N. Am. Fungi, 1851, *A. B. Lan-glois*); No date, III, no locality (Ravenel's Fungi Caroliniani, 89, no collector recorded).

On *Spartina patens* (Ait.) Muhl. 1891, III, Salem, N. J. (*A. Commons*); Sept. 1898, III, Madison, Conn. (2067, *T. E. Hazen*).

In many parts of the country, especially in the upper Mississippi valley, this species is one of the most abundant of plant

rusts, both on *Spartina* and *Fraxinus*. Bessey⁶ records that in 1885 it infested the green ash trees about Lincoln, Neb., to such a degree as to attract the attention of casual passers.

The teleutosporic form is equally common with the aecidial, and is well represented in herbaria, where it has passed under the name of *Puc. Phragmitis* for the most part. It was not until the publication of the result of cultures by the writer⁷ about two years ago, that the autonomy of the species was recognized.

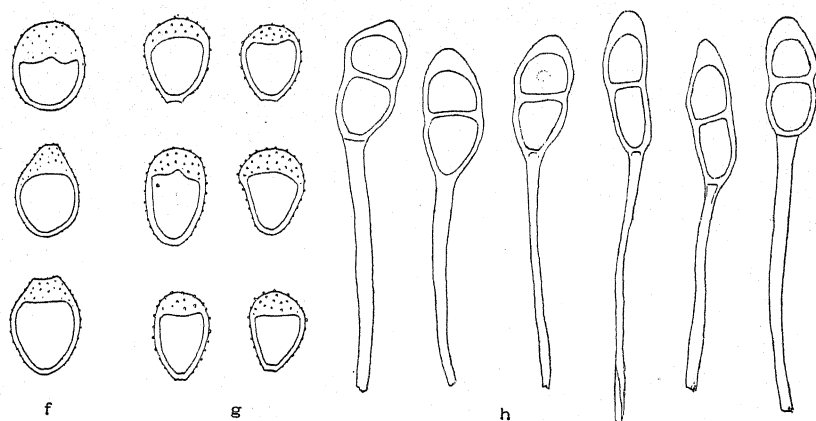


FIG. 2.—*P. Fraxinata*: *f*, three aecidiospores on *Fraxinus lanceolata*; *g*, six uredospores, and (*h*) six teleutospores, both on *Spartina cynosuroides*.

The uredo form is very rarely collected, and the writer has had much difficulty to secure material for study. The sori are rather conspicuous when they first appear, but are usually not abundant, and are soon replaced by the teleutospores.

The aecidiospores and uredospores show a very remarkable similarity in color, form, and markings (*fig. 2, f and g*). Both have colorless walls, greatly thickened at the apex, and evenly tuberculate. The contents are of the same shade of orange, a color that speedily disappears with the death of the protoplasm. In fact the uredospores differ in appearance from the aecidiospores chiefly in being a little more robust. The shape and dimensions in the diagnosis above are for the spores when seen

⁶ Amer. Nat. 19:886; see also *ibid.* 20:806. ⁷ Bot. Gaz. 29:275.

from the side, that is, in vertical section, making the description of both forms comparable with that of the teleutospores (*fig. 2, h*).

On *Spartina* this rust occurs exclusively on the hard and smooth surfaces of the plant; the under (smooth) side of the blade, the sheaths, and the exposed parts of the internodes. On *Spartina polystachya* and *S. glabra* it grows equally well on both surfaces of the blade. This difference of habit is correlated with the fact that in these two hosts the hard tissues of the leaf are almost equally well developed upon both sides of the blade, so much so as to prevent the leaf from becoming much convolute upon drying, as it does in the other species of the genus.

The writer is fortunate in having been able to examine all the type material upon which the synonymy of the species is based. The type of *Aecidium Fraxini* Schw., which is in the Schweinitz collection at the Philadelphia Academy of Sciences, consists of a single leaf, bearing thirteen round groups of aecidia. The spots are much swollen, but too young to show open peridia. The type material of *Uredo peridermiospora* Ellis & Tracy consists of the bases of two similar leaves of *Spartina glabra* Muhl., one of which is in the herbarium of Mr. S. M. Tracy, the collector, and the other is in the Ellis herbarium at the New York Botanical Gardens. In the packet at the latter place is the following unsigned note: "Spor. pyriform, $35-45 \times 18-22 \mu$, contents orange-red with a hyaline envelop, which is at first subtubercular-roughened, but finally becomes smooth or nearly so. The spores are much like those of *Peridermium pyriforme* Pk." The type of *Puccinia sparganioides* E. & E. is in the Ellis herbarium at the New York Botanical Gardens. It consists of quite a number of portions of leaves, each about 10^{cm} long, all well covered with uredo- and teleutosori, and is accompanied by diagnostic and other notes. The host was at first supposed to be *Carex sparganioides*, and was so stated in connection with the original description, and hence the specific name; it was afterward thought to be *Carex stricta*, and is so labeled in Ellis and Everhart's N. Amer. Fungi, no. 3475; finally the host was

determined as *Spartina cynosuroides*, and the correction published by Bartholomew⁸ in his list of Kansas Uredineae. All the synonyms of the species are founded upon these three types.

The oldest specific name, *Fraxini*, cannot be transferred to the genus *Puccinia*, as there is already a *P. Fraxini* Kom. from the orient,⁹ and the next oldest name, that of Link, is therefore taken.

3. *Puccinia Seymouriana*, sp. nov.

EXSICC: Ellis & Everhart, N. Am. Fungi, 1474^{III}.

Seymour & Earle, Econ. Fungi, 69^{III}.

O. I. Spermogonia and aecidia unknown.

II. III. Sori epiphyllous, intercostal, prominent, oblong, ruptured epidermis inconspicuous. II. Uredospores globose, or broadly elliptical, 26–39 by 30–45 μ , contents orange when fresh, becoming faintly yellow when old, at first globose, afterward angular and shrunken, wall colorless, thickened above, sometimes to more than half the diameter of the spore, prominently tuberculate, pores obscure. III. Teleutosori pulvinate, chocolate brown; teleutospores elliptical or oblong, 20–26 by 37–52 μ , slightly constricted at the septum, apex obtuse, thickened; pedicel firm, slender, tinted, once to thrice the length of the spore.

From Massachusetts to Illinois and Iowa, and northward. On blades of *Spartina cynosuroides*; uredospores in July, soon followed by the teleutospores which persist through the winter and germinate the next spring. Specimens have been examined as follows:

On *Spartina cynosuroides* (L.) Willd. July 1881, III, Hudson, Ill. (2348, *A. B. Seymour*); Aug. 1881, III, English prairie, Ill. (1346, *A. B. Seymour*); Oct. 1881, III, Canton, Ill. (1771, *A. B. Seymour*); Oct. 1881, May and Sept. 1882, III, Normal, Ill. (1829, 4794, 6262, *A. B. Seymour*); June 1882, III, Normal, Ill. (5272, *C. A. Hart*); Jan. and March 1883, III, Normal, Ill. (*C. A. Hart*); April 1883, III, Madison, Wis. (*Wm. Trelease*); Oct. 1883, III, Chicago, Ill. (*J. C. Arthur*); Nov. 1883, III, Normal, Ill. (Ellis & Ever-

⁸Trans. Kan. Acad. Sci. 16: 178.

⁹See Jaczewski, Komarov, Tranzschel, Fungi Rossiae Exsiccati, no. 225, where full description is given.

hart's N. Am. Fungi, 1474, *A. B. Seymour*); Aug. 1884, III, Bismarck, N. D. (Jour. to Wash. Terr., 296, 302, *A. B. Seymour*); Oct. 1890, III, North Weymouth, Mass. (Seymour & Earle's Econ. Fungi, 69, *L. M. Underwood*); Aug. 1896, III, Pt. Abino, Ontario. (*S. M. Tracy*); Sept. 1899, ii. III, Racine, Wis. (type collection, *J. J. Davis*); April 1899, Mar. and April 1900, April 1901, III, Racine, Wis. (*J. J. Davis*); No date, III, Ames, Iowa (*L. H. Pammel*).

In naming this very distinct new species I take pleasure in recognizing the services of Mr. A. B. Seymour in the cause of mycological science. One-third of the collections of this species that I have been enabled to study, coming from various sources, were made by him, and it was during my examination of the material in his private herbarium, kindly placed at my disposal, that I became aware of the existence of the species, which has heretofore been an unrecognized part of the preceding one.

The species is separable from *P. Fraxinata*, and recognizable with considerable ease, by the position of the teleutosporic sori on the rough side of the leaf, emerging from between the nerves. They are usually a little lighter in color also. But the final reliance must be upon the uredospores (*fig. 3, k*), which are very distinctive, and a few of which may almost invariably be found intermixed with the teleutospores (*fig. 3, l*), at whatever season of the year the material may have been gathered. The shrunken contents lying at the base of the spore, and the colorless, tuberculate wall, gives the spores a wholly unique appearance among gramineous species.

Attempts at cultures have been made for three seasons past, but so far in vain. At first the efforts were misdirected from lack of any but the vaguest geographical clues. After detecting and establishing a connection between morphological similarity in uredo and aecidium and also a specific relationship in the preceding species, I searched through the herbarium for some aecidiosporic form having colorless, tuberculate walls, and angularly shrunken contents, and was rewarded by finding that *Aecidium Cephalanthi* Seym. possessed exactly these characters. Its geographical range is also that of *P. Seymouriana*, so far as the two are known. In the spring of 1901 I was possessed of

this information and the necessary material, but was frustrated by failure of the teleutospores to germinate. The preceding winter seems, for some unknown reason, to have been destructive of many plant rusts. Not only this species, but *P. Asparagi*, *P. lateripes*, *P. emaculata*, *P. vexans*, and many others could not be made to germinate, showing that the spores had winter-killed. Although cultures must be awaited, yet there can be little doubt that the early stages of *P. Seymouriana* occur upon *Cephalanthus*.

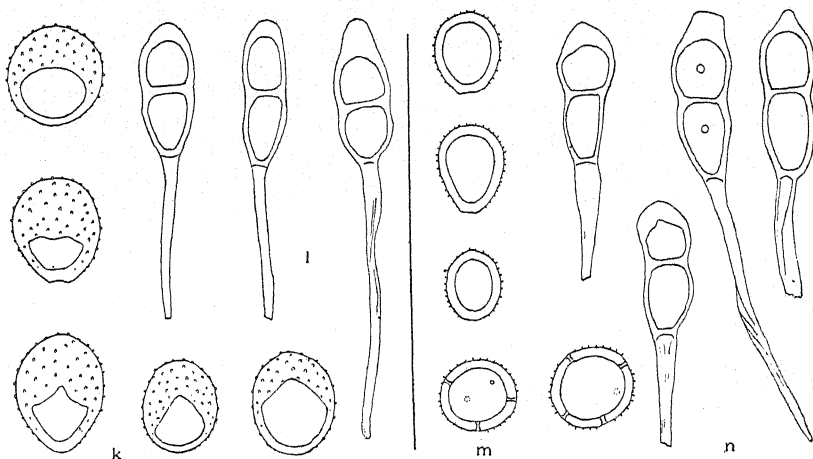


FIG. 3.—*P. Seymouriana*: *k*, four uredospores, and (*l*) three teleutospores, on *Spartina cynosuroides*. *P. Distichlidis*: *m*, five uredospores, the two lowermost shown in transverse optical section, and (*n*) four teleutospores, both on *Spartina gracilis*.

4. PUCCINIA DISTICHLIDIS E. & E. 1893. Proc. Phil. Acad. Sci. 1893: 152.

SYN.: 1898. *Dicaeoma Distichlidis* Kuntze. Rev. Gen. Pl. 3: 468.

O. I. Spermogonia and aecidia unknown.

II. III. Sori epiphyllous, intercostal, early naked, ruptured epidermis conspicuous. II. Uredospores broadly elliptical, broadly obovate or globose, 26–32 by 27–40 μ , wall pale yellow, thick, abundantly echinulate with stout points, pores six or more, scattered, indistinct, contents sometimes centrally shrunken. III. Teleutosori blackish, prominent, linear-lanceolate with acute ends; teleutospores obovate or lance-oblong, 17–21 by 48–56 μ ,

slightly constricted at the septum, apex obtuse or subacute, thickened, side walls thin, base somewhat narrowed, pedicel firm, rather thick, tinted, as long as the spore or longer.

From Montana to North Dakota and Iowa. On blades of *Spartina*; uredospores in July, soon followed by the teleutospores, which persist through the winter. Specimens have been examined as follows:

On *Spartina gracilis* Trin. Oct. 1888, III, Ten-mile creek, Mont. (*F. W. Anderson*); Oct. 1888, III, Helena, Mont. (185 *F. W. Anderson*); Oct. 1888, III, Helena, Mont. (*F. D. Kelsey*); Aug. 1890, ii, III, Helena, Mont. (*F. D. Kelsey*); Sept. 1891, III, Helena, Mont. (type collection, *F. D. Kelsey*); Aug. 1901, III, near Laramie, Wyo. (1219, *Elmer D. Merrill* and *E. N. Wilcox*).

On *Spartina cynosuroides* (L.) Willd. Aug. 1884, III, Valley city, N. D. (Journey to Wash. Terr., *A. B. Seymour*); Aug. 1886, III, Emmet co., Iowa (544 *R. J. Cratty*); May 1899, III, Fargo, N. D. (*H. L. Bolley*); July 1899, II, III, Fargo, N. D. (*H. L. Bolley*).

This species was described some time ago, but its true character and position have remained unrecognized, on account of error in determination of the host, which was said to be *Distichlis maritima*, and hence the specific name. The unfortunate mistake has led to much confusion, as many collections on *Distichlis* have been given this name by wrong assumption, and many unwise comparisons made.

The type is in the Ellis collection at the New York Botanical Garden. It consists of several portions of leaves, each about 8^{cm} long, well covered with teleutosori. It was gathered September 21, 1891, at Helena, Mont., by Rev. F. D. Kelsey. In the herbarium of Mr. A. B. Seymour are two other collections from the type locality, and in the herbarium of Dr. W. G. Farlow is a fourth collection from the same locality. A comparison of these several collections, one (*Anderson's* No. 185) being accompanied with inflorescence, leaves not the shadow of a doubt that the host for all of them is *Spartina gracilis* Trin. There is, however, a *Puccinia subnitens* Diet., a wholly distinct species, which does occur upon *Distichlis maritima*.

The pointed extremities of the teleutosori, and the large

echinulate uredospores, with uncontracted or occasionally centrally contracted contents, well distinguish this species from other *Spartina* rusts (fig. 3, *m* and *n*).

5. PUCCINIA RUBELLA (Pers.), nom nov.

SYN.: 1791. *Aecidium rubellum* Pers. Linné Syst. Nat. cur. Gmelin 2: 1473.

1796. *Aecidium Rumicis* Hoffm. Bot. Taschenb. 2: —.

1803. *Uredo Phragmitis* Schum. Fl. Saell. 2: 231.

1808. *Puccinia arundinacea* Hedw. Lam. and DC., Encycl. 8: 250.

1810. *Uredo striola* Strauss. Wetter. Annal. 2: 105.

1827. *Uredo rubella* Spreng. in part. Syst. Veg. 4: 572.

1876. *Puccinia Phragmitis* Körn. Hedw. 15: 179.

1898. *Dicaeoma Phragmitis* Kuntze. Rev. Gen. Pl. 3: 470.

EXSICC.: Sydow, Ured., 278^I, 576^{III}, 679^I, 680^I, 779^I, 924^I.

Seymour and Earle, Econ. Fungi, 70^{III}.

Carleton, Ured. Amer. 36^{III}.

Eriksson, Fungi Par. Scand. Exsicc., 169^I.

Linhart, Fungi Hungar., 26^{II} ^{III}, 37^I.

Vize, Fungi Brit., 124^{III}, 161^I.

Thuemen, Myc. univ., 630^I.

O. I. *Spermogonia* not observed. *Aecidia* small, hypophyllous, on purple-red, somewhat swollen spots, in rounded, often circinating groups, peridia white, low, with reflexed, much split border, aecidiospores polygonal, 17–25 μ in diameter, nearly colorless, wall rather thin, finely tuberculate.

II. III. Sori amphigenous, prominent, oblong, elongated on sheaths and stems, ruptured epidermis inconspicuous. II. Uredosori, brownish-yellow, pulverulent, without paraphyses; uredospores elliptical or obovate, 19–24 by 27–36 μ , wall thick, golden yellow, tuberculate, pores four, equatorial. III. Teleutosori very prominent, blackish-brown; teleutospores oblong, rounded or obtuse at both ends, slightly constricted at the septum, 18–24 by 45–64 μ , side walls rather thick, apex a little thickened, pedicel firm, slender, strongly tinted, very long, two to five times the length of the spore.

The northern United States east of the Rocky mountains, and Europe. Early stages on several species of *Rumex*, not yet collected in America, but cultivated from American teleuto-

spores, and also on *Rheum*; later stages on *Phragmites*. Besides many European specimens the following from America have been examined:

On *Rumex crispus* L. May, 1899, I, Lafayette, Ind. (cultivated by the writer from teleutospores sent from Wisconsin and Nebraska.)

On *Rumex obtusifolius* L. May, 1899, I, Lafayette, Ind. (cultivated by the writer from teleutospores sent from Wisconsin and Nebraska.)

On *Rheum Rhaiponticum* L. June, 1901, Kearney, Neb. (1822, *J. M. Bates*).

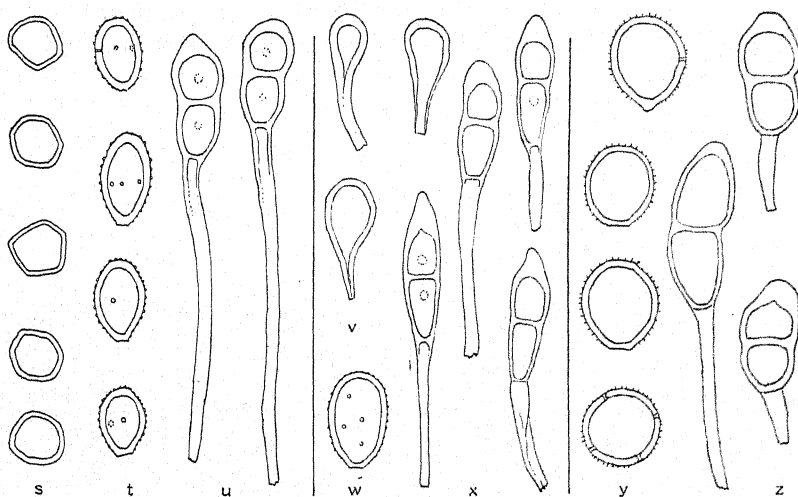


FIG. 4.—*P. rubella*: *s*, five aecidiospores on *Rumex obtusifolius*, cultivated; *t*, four uredospores, and (*u*) two teleutospores, both on *Phragmites*. *P. similima*: *v*, three paraphyses from uredosori; *w*, one uredospore; *x*, four teleutospores, all on *Phragmites*. *P. Arundinariae*: *y*, four uredospores, the lowermost in transverse section; *z*, three teleutospores, both on *Arundinaria*.

On *Phragmites Phragmites* (L.) Karst. (*P. communis* Trin.) Aug. 1881, III, McHenry, Ill. (1325, *A. B. Seymour*); Aug. 1881, III, Elgin, Ill. (1368, *A. B. Seymour*); Oct. 1884, III, Mason city, Ia. (*E. W. D. Holway*); Oct. 1885, III, Decorah, Ia. (*E. W. D. Holway*); July, 1886, II, III, Vermillion lake, Minn. (137, *E. W. D. Holway*); Oct. 1892, III, Coolidge, Kan. (*Carleton's Ured. Amer.*, 36, *M. A. Carleton*); Nov. 1893, III, Wilmington, Del. (*A. Commons*); Apr. 1899, III, Racine, Wis. (partly used by the writer for successful cultures on *Rumex*, *J. J. Davis*); May, 1899, III, Lincoln, Neb. (partly used by the writer for successful cultures on *Rumex*, *C. E. Bessey*); 1901, III, Callaway, Neb. (1658, *J. M. Bates*).

This cosmopolitan species shows no American peculiarities (fig. 4, s, t, and u) except the great rarity of the aecidial form. The teleutospores, however, are strongly viable, and grow readily on *Rumex crispus* and *R. obtusifolius*, forming normal aecidia exactly like those collected in the open in Europe.¹⁰ The aecidia, which are small, colorless, and inconspicuous, have so far only been found once with certainty in America.

The reasons for selecting the name here adopted should probably be stated. There is no question but that Persoon's *Æcidium rubellum* included the aecidial form of this species of Puccinia, and that it is the oldest name. His diagnosis ran as follows: "*Ae. rubrum. a rumicis, thecis congestis seminibusque albis. β grossulariæ, thecis sparcis seminibusque pallidis.*" The name might evidently have been written *P. Rumicis*, had that name not already been applied elsewhere. In writing *P. rubella* it is assumed that, when all the forms composing a species are serially separated, as indicated by letters or otherwise, the specific name covers the first of these varieties, whether this first variety is given a distinctive name or not. If in such a case the varieties are erected into species, the first one may bear either the specific or the first varietal name.

6. *Puccinia simillima*, sp. nov.

EXSICC.: Sydow, Ured., 274^{III} in part.

O. I. Spermogonia and æcidia uncertain.

II. III. Sori amphigenous, low and rather small, oblong, elongated on sheaths, ruptured epidermis somewhat noticeable. II. Uredosori light yellow, pulverulent, with clavate paraphyses; uredospores obovate or oblong-clavate, 18–22 by 26–44 μ , wall of medium thickness, golden yellow, minutely tuberculate and sometimes slightly echinulate, pores indistinct, scattered, number undetermined. III. Teleutosori small, very numerous, nearly or quite black; teleutospores at first arising from the uredosori, linear-oblong or oblong-lanceolate, very little constricted at the septum, 15–20 by 42–56 μ , base narrowed, side walls thin, apex acuminate, acute or less often obtuse, thick-

¹⁰ARTHUR, BOT. GAZ. 18: 269–270. Ap 1900.

ened up to 15μ , pedicel firm, thick, the length of the spore more or less.

Iowa and Wisconsin. On blades and sheaths of *Phragmites*; uredospores in July, soon followed by teleutospores, which persist through the winter. Specimens have been examined as follows:

On *Phragmites Phragmites* (L.) Karst. (*P. communis* Trin.) Dec. 1883, III, Spirit lake, Ia. (*J. C. Arthur*); Oct. 1884, III, Mason city, Ia. (*E. W. D. Holway*); Oct. 1885, III, Decorah, Ia. (Sydow's Uredineen, 274, *E. W. D. Holway*); Sept. 1892, III, Ames, Ia. (*G. W. Carver*); Aug. 1898, II. iii, Spirit lake, Ia. (type, *J. C. Arthur*); May 1899, III, Armstrong, Ia. (*R. I. Cratty*); Sept. 1901, III, Racine, Wis. (*J. J. Davis*).

This species probably has a wider distribution than the above series of specimens indicate, as it is likely to have been overlooked. It occurs frequently intermixed upon the same leaves with *P. rubella*. This was the case with all the above collections, except those from northwestern Iowa, at Spirit lake and Armstrong.

Cultures have not yet been made, but there are the strongest reasons, based upon field observations, for believing that the aecidial stage occurs upon *Anemone Canadensis* L. (*A. Pennsylvanica* L.).

The species is very closely related to *P. Magnusiana* Körn.; and even the supposed aecidial stage on *Anemone* resembles the aecidial form of that species on *Ranunculus repens* and *R. bulbosus*. It is distinguished, however, by the slender, pointed teleutospores, and by the more clavate and less roughened uredospores, and probably by the aecidial host (*fig. 4, w* and *x*).

7. PUCCINIA ARUNDINARIAE Schw. 1822. Schrift. d. Nat. Ges. zu Leipzig 1: 72.

SYN.: 1898. *Dicaeoma Arundinariae* Kuntze. Rev. Gen. Pl. 3: 467.

O. I. Spermogonia and aecidia unknown.

II. III. Sori hypophyllous, rather small, nearly round, early naked, ruptured epidermis inconspicuous. II. Uredosori cinnamon-brown, pulverulent, without paraphyses; uredospores large, broadly elliptical or globose, $24-32\mu$ in diameter, wall

rather thin, brownish-yellow, sparingly echinulate with stout points, pores indistinct, apparently four and equatorial. III. Teleutosori pulvinate, solid, blackish brown; teleutospores dark brown, linear-oblong, 20-24 by 48-72 μ , not constricted at the septum, side walls moderately thick, apex somewhat thickened, obtuse or rounded, pedicel slender, firm, slightly tinted or colorless, as long as the spore, more or less.

In the southern states from North Carolina to Alabama, not common. On leaves of *Arundinaria*. Specimens have been examined as follows:

On *Arundinaria tecta* (Walt.) Muhl. No date, III, Salem, N. C. (type, *L. Von Schweinitz*); Feb. 1896, III, Auburn, Ala. (*F. S. Earle* and *L. M. Underwood*); Sept., 1897, III, Tuskegee, Ala. (95, *G. W. Carver*); Sept. 1899, II, iii, Clemson College, S. C. (54, *P. H. Rolfs*); Dec. 1900, III, Clemson College, S. C. (*P. H. Rolfs*).

This is not an abundant species. Although collected by *L. von Schweinitz* in North Carolina about 1820, and again later in Philadelphia, Penn.,¹¹ on plants in the Bartram Gardens, brought from a distance, yet it has been rarely collected since. It appears to occur over a wide area, but at all times very sparingly. The uredo stage, being light brown in color, is especially difficult to find. I am indebted to Mr. *P. H. Rolfs* and Mr. *George W. Carver* for material for study, which they obtained for me after much search.

The type specimen in the herbarium of the Philadelphia Academy of Sciences consists of a single fragment of leaf about 8 by 50 mm, bearing only three sori. Both host and fungus fall somewhat short of perfect development.

A single glance at the uredospores of this species (*fig. 4, y*) shows that it could be associated with *P. rubella* (*P. Phragmitis*) only through ignorance of its real characteristics. The usually elongated, non-constricted, and often curved teleutospores are also distinctive (*fig. 4, z*).

This completes the list of species known to occur on *Spartina*, *Phragmites*, and *Arundinaria* in North America. There are only

¹¹Trans. Amer. Phil. Soc. 4: 295.

two records¹² of any Uredineae being found on these hosts in South America, both given as *P. Phragmitis*, which I have had no opportunity to verify; and there is no record of such occurrence in Central America, Mexico, or the West Indies.

The parasitism of the Uredineae is so intimate that, when it is noticed that the three genera of hosts here studied belong to three widely separated sections of Gramineae, strong proof should have been required to show that any one species of rust could inhabit them all. In determining unnamed material the following key, based upon distinctions of host, position on the host, and the uredospores may prove serviceable. It is rare that some search in almost any specimen, at whatever time of year it may be gathered, does not disclose at least a few uredospores. The teleutospores are not so distinctive.

CHLORIDÆ: *Spartina*.

Sori arising from soft tissues (intercostal),

Uredospores with wall thin, colored, echinulate - *U. acuminatus*.

Uredospores with wall thick, pale, echinulate - *P. Distichlidis*.

Uredospores with wall thickened above, colorless,
tuberculate - - - - - *P. Seymouriana*.

Sori arising from hard tissues (supercostal),

Uredospores with wall thickened above, colorless,
tuberculate - - - - - *P. Fraxinata*.

FESTUCEÆ: *Phragmites*.

Sori amphigenous, uredosori without paraphyses,

Uredospores with four equatorial pores - - - *P. rubella*.

Sori amphigenous, uredosori with paraphyses,

Uredospores with indefinite, scattered pores - - *P. simillima*.

BAMBUSEÆ: *Arundinaria*.

Sori hypophyllous, uredosori without paraphyses,

Uredospores with rather thick wall, echinulate - *P. Arundinariae*.

The four species on *Spartina* will shortly be published as *exsiccati* in the fourth fascicle of Arthur and Holways's *Uredineae Exsiccatae*; and the two species on *Phragmites* will be published somewhat later in the fifth fascicle of the same series.

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¹²Hedwigia 35:288. 1896. SPEGAZZINI's Fungi Arg. 1221. 1899. Both reported on *Phragmites* from Argentine.

CONTRIBUTIONS FROM THE ROCKY MOUNTAIN HERBARIUM. III.

AVEN NELSON.

STUDIES IN ERIOGONUM.

THIS genus is remarkably well represented in Wyoming. Since most of the species in it are peculiar to arid America, any of the states with desert areas may be expected to represent a considerable number of the increasingly long list of species. A line drawn from central Wyoming to western Arizona will divide into somewhat equal parts the Eriogonum belt.

No recent revision of the genus has been published, but a considerable number of new species have appeared. When one considers how extensively collections have been made in the arid west indicated above, it seems rather remarkable that Dr. Watson's revision of twenty-five years ago (Proc. Am. Acad. 12:254) should so nearly represent our knowledge of these plants as it does. That a revision is now needed I think all will admit, but until some one finds time and occasion to do so, notes upon and additions to the species may not be out of place.

Eriogonum orendense, n. sp.—Caudex woody, almost wholly subterranean, its numerous branches densely tufted: tomentum rather dense, uniform throughout the plant, giving it a greenish-white hue: stems numerous, crowded, very short, exclusive of the woody persistent base not to exceed 5^{cm}: leaves numerous, crowded, narrowly oblong or oblanceolate, subacute, 1–3^{cm} long, tapering into a slender petiole which usually exceeds the blade: scapes erect, 7–15^{cm} long, surpassing the leaves: inflorescence umbellate, with short subulate bracts; the rays unequal, 1–2^{cm} long, terminating in a few-flowered cyme (3–7), with very short connate bractlets: involucre short-peduncled (1–3)^{mm}, turbinate, merely toothed around the summit, about 3^{mm} long, many-flowered (8–12): calyx bright yellow; the segments

similar, scarcely 2^{mm} long, oblong, obtuse, the slender pedicels intermingled with setae bearing stipitate glands and a few fine slender hairs: filaments linear, sparsely pubescent to above the middle: styles slender, long exserted: ovary glabrous; mature akene not seen.

Probably most nearly allied to *E. campanulatum* Nutt., though very different from that and blossoming much earlier in the season. The proposed species was found in full bloom June 11, 1900, on the stony slopes of Orendo butte, in the Red desert. This is very early in the growing season in this range. *E. campanulatum*, in this same range, blossoms late in the season, and is a much larger plant, with a compound inflorescence as well as a number of minor floral differences. The type no. is 7143, collected as above.

ERIOGONUM OVALIFOLIUM Nutt.—There is perhaps no species in the genus more variable as to color of flowers than this, if the specimens as named in the herbaria are to be considered the only evidence. Nuttall originally distinguished two species in the present aggregate and consistently maintained them both. *E. ovalifolium* was applied to the form with "bright sulphur-yellow" perianth, which occurs in greater or less abundance on the arid table-lands about the "sources of the Missouri." Of the allied forms, however, this was the less abundant, so that by this time the mention of *E. ovalifolium* suggests not the original, but the *E. purpureum* of Nuttall. That this is the case is easily verified by referring to Jour. Acad. Philad. 7: 50, and to Jour. Acad. Philad. new ser. 1: 166, in the latter of which these two species appear under the there proposed genus *Encycla*.

Whether the two can be maintained as distinct species may well be questioned, but there are the best of reasons for retaining the later one as a variety. Not the color of the perianth alone, though in regions in which both grow I have seen nothing to indicate that they intergrade, but the differences (though slight) as given in the publications cited indicate at least varietal rank, as suggested in DC. Prod. 14: 10. Accordingly the white-flowered form, which almost constantly shows traces of purple or may even become of a deep purple hue (never yellowish?), may be designated

ERIOGONUM OVALIFOLIUM purpureum, n. comb.—*Encycla purpurea* Nutt. Jour. Acad. Philad. new ser. 1: 166; DC. Prod. 1. c.

ERIOGONUM CRASSIFOLIUM Benth. Trans. Soc. Linn. Lond. 17: 408; Hook. Fl. Bor.-Am. pl. 176. *E. aureum* Nutt. in. DC. Prod. 14: 8.—This excellent species has for a long time been wholly in eclipse, or at most has been accorded only varietal rank. It is most abundant in the type locality, "Scopulosis ad regionem super. fl. Platte." It has several times been collected by the writer and distributed as a variety of *E. flavum* Nutt. Again collected in 1900 as no. 7285 in quantity, and will be distributed as a species, which it properly is.

ERIOGONUM CRASSIFOLIUM tectum, n. var.—Densely tufted with deep set woody roots, the crowns of the branched caudex inordinately enlarged by the thick, closely sheathing, very woolly leaf bases: leaves all crowded on the short crown, firm and thick, densely tomentose, ovate to oval or more rarely oblong, 2–3^{cm} long, on very short petioles ($\frac{1}{4}$ to $\frac{1}{2}$ as long): scapes stout, about 1^{dm} long: flower yellow, but the yellow obscured by the long, dense, tomentose pubescence of the involucre and calyx-segments: inflorescence subcapitate, the rays mostly shorter than the foliar bracts.

The variety may readily be known by the remarkable protection against desiccation and cold that is afforded the crowns of the caudex, and the whole plant for that matter, by the dense tomentum. That is a character of the species, but in a small degree when compared with the variety. The shorter petioles and rays and the thick, leathery leaves further distinguish it. The species comes into blossom in June, while the variety in the same range not till August. Only one no. of the variety is at hand, 2041, Sand creek, Albany co., Aug. 8, 1896, on dry, sandy, eroded banks.

Eriogonum fruticosum, n. n.—*E. aureum* Jones, Contrib. to W. Bot. 7: 718; not *E. aureum* Nutt. DC. Prod. 14: 8.

ERIOGONUM FRUTICOSUM ambiguum, n. comb.—*E. aureum ambiguum* Jones, Contrib. to W. Bot. 7: 719.

ERIOGONUM FRUTICOSUM glutinosum, n. comb.—*E. aureum glutinosum* Jones, Contrib. to W. Bot. 7: 719.

Eriogonum laxifolium.—*E. Kingii laxifolium* T. & G. Proc. Am. Acad. 8: 165; *E. chrysocephalum* Gray, Proc. Am. Acad. 11: 101

Malvastrum dissectum, n. comb. — *Sida dissecta* Nutt., Torr. & Gray, Fl. 1:235; not *Malvastrum coccineum* Gray, Pl. Fendl. 24; Gray, Pl. Wright. 1:17; nor *M. dissectum* Cockerell, Bull. Torr. Bot. Club 27:87. — Perennial: many-stemmed from a multicipital caudex, 2^{dm} high or less, densely cinerously stellate-pubescent, the stems whitened with the closely appressed hairs, the calyx obscurely glandular beneath the pubescence: leaves small, 1–3^{cm} broad, pedately 3–5-parted, the divisions incisely lobed, the lobes narrowly oblong to linear: racemes several-flowered, pedicels 2–5^{mm} long; flowers scarlet: the petals obovate, nearly truncate and merely emarginate; the stigmas capitate.

That Nuttall was justified in separating this from *M. coccineum* seems perfectly evident to any one who has seen both species in their native habitat. It is at once distinguished from *M. coccineum* (Nutt.) Gray by its cinereous white aspect, by its smaller and more narrowly lobed leaves, and narrower petals. There can be no question which species Nuttall meant to designate *Sida dissecta*, when one reads the notes and descriptions relating to these two species in *Fl. N. Am.* The *Cristaria coccinea* Pursh, Fl. 2:453, *Malva coccinea* Nutt. Gen. 2:81, and *Sida coccinea* T. & G. Fl. 235, undoubtedly refer to the same plant, viz., the broad-leaved form so common on the great plains between the Rocky mountains and the Missouri river. *Sida dissecta* of the T. & G. *Flora* is clearly the plant still found on the high saline desert table-lands, "sources of the Platte near the Rocky mountains." Were more evidence needed to show that *S. dissecta* designates the more western plant, it is found in the fact that the *Sida dissecta* Hook. and Arn. Bot. Beechy, Suppl. 326, is considered by Torrey and Gray (Fl. N. A. 682) as identical with the Nuttallian plant.

On the other hand, Dr. Gray did not consider the plants of *Pl. Fendl.* and *Pl. Wright.* as identical. In the former he uses this expression " * * a few specimens of the var. *dissecta*, or of forms that evidently connect the *Sida dissecta* of Nuttall with *S. coccinea*." In the latter, the language is " * * a more canescent variety, * * approaching the var. *dissectum*."

These southern narrow-leaved forms, nicely distinguished from *Malvastrum coccineum* by Professor Cockerell, are far enough from the Nuttallian *dissectum*. They may therefore be designated —

Malvastrum Cockerelli, n. n. — *M. dissectum* (Nutt.) Cocker-

ell, Bull. Torr. Bot. Club 27:87. *M. coccineum dissectum* Gray, Pl. Fendl. 24; and Pl. Wright. 1:17.

Malvastrum elatum. — *M. coccineum elatum* E. G. Baker, Jour. Bot. 29:171. — This plant, originally published as a variety, is so different from the true *M. coccineum* that it is less confusing to consider it a species. It is not only much larger, with broader leaf-segments, but its more erect habit and tendency to paniculate branching give it the aspect of a *Sphaeralcea*. Its pubescence is less conspicuous, and the carpels not so evidently reticulate-veined, and the sepals shorter and more abruptly acute. It occurs very sparingly. I have twice collected it, both times at Evanston, Wyoming.

CERASUS DEMISSA melanocarpa, n. var. — Varying from a small shrub to a tree-like one, 4-5^m high: leaves smooth or nearly so on both sides, the teeth of the fine serration incurved or appressed; petioles not glandular: raceme of white flowers compact, erect or ascending: fruit when fully mature black.

The Rocky mountain form of *Cerasus demissa* is clearly, at least varietally, distinct from the original Nuttallian specimens. Nuttall's specimens from "The plains of the Oregon towards the sea, and at the mouth of the Wahlamet," differ from the more eastern form in the pubescent leaves which are serrate with straight teeth and with glandular petioles; more evidently yet in the red fruits which are sweeter and less astringent than the black ones.

The variety proposed is in many respects intermediate between typical *Cerasus virginiana* of the eastern states and typical *C. demissa* of the far west. All the Rocky mountain specimens seen by me are of this variety.

GENTIANA BRACTEOSA Greene. — In publishing this species (Pitt. 4:180) Professor Greene lays stress upon the narrowness of the leaves, but I am satisfied that this character will not distinguish it from *G. Parryi*. Some fine specimens collected by Mr. H. N. Wheeler, Camp Albion, Colorado, Aug. 30, 1901, have the floral characters of *G. bracteosa*, but typical leaves of *G. Parryi*. Furthermore, in some specimens of *G. Parryi* the stems in the same clump vary as to the leaves from narrowly oblong to broadly ovate. The species I think will stand, however, on the bract characters, and a peculiarity of the spathaceous cleft calyx not pointed out by Dr. Greene. The calyx-tube

is membranous at summit, and its oblong or elliptic short green teeth are seemingly not a continuation of the tube, but are inserted below the margin, on the outside, and often scarcely exceeding its membranous rim. Unless these characters are distinguishing, it will have to take varietal rank.

Gentiana strictiflora (Rydb.).—*G. acuta strictiflora* Rydb. Mem. N. Y. Bot. Gard. 1: 309. 1900; full citation given in the same place.—This well deserves specific rank. It has quite as good characters as the allied species *G. acuta*, *G. tenella*, and *G. heterosepala*. Its large size, strict habit, numerous flowers, and the distinctly ochroleucous corollas are wholly characteristic. Common in moist swales on bottom lands.

GENTIANA CALYCOSA xantha, n. var.—Habit of the species, smaller, 1^{dm} or less high: leaves about five pairs, longer than the internodes; the single flower smaller, yellow or yellowish-white with numerous green dots.

At first sight these plants strike one as a decided novelty, but closer examination reveals no decisive character except the color. Even the conspicuous green dots in the corolla are not wanting in the species itself, though much obscured by the deep blue of that.

Collected by Elmer D. Merrill and E. N. Wilcox, on the Tetons, above Leigh's lake, Wyoming, July 26, 1901; no. 1108.

Phacelia corrugata, n. sp.—Biennial or more enduring, 3–5^{dm} high, slightly glutinous and more glandular-pubescent: stem either branched or simple at base, the branches also sparingly branched, moderately leafy, terminating in elongated naked peduncles: leaves narrowly oblong in outline, somewhat alternately 11–15-lobed, the broad sinuses extending about half way to the midrib, each lobe with two to four rounded unequal lobules; petioles short or wanting: spikes very dense even in fruit, rather tardily open; pedicels very short (1^{mm}): sepals linear-oblancoolate, sparsely hirsute, nearly as long as the corolla: corolla blue, campanulate-funnelform, 1^{cm} or more long, as much in diameter over the limb, lobes suborbicular, internal folds short and united around the base of the filament: stamens and styles nearly twice the length of the corolla; the undivided base of the style pubescent: capsule elliptical, about 5^{mm} long: the seed oblong,

obtuse at both ends, deeply excavated on the ventral side, the inner side of the lateral angles and one side of the salient central ridge strikingly corrugated by rounded, pitted papillae, minutely ridged-papillate on the base.

This has passed for a form of *P. crenulata* Torr., a plant which I think is found only much farther west. That differs from the plant here described in the smaller size, more deeply lobed leaves, more open spikes, rotate-campanulate, violet corolla, with broad internal folds; the short, linear calyx-lobes; the globular capsule and reticulated, much smaller seeds.

I base the species on specimens from Colorado as follows: no. 2129 (type), G. E. Osterhout, Rifle, Garfield co., June 23, 1900, in mature fruit; (co-type) C. S. Crandall, Palisades, Mesa co., May 14, 1898, in full bloom.

Gilia Merrillii, n. sp.—Perennial, from a short woody caudex and tap root: stems few to many from the crown, erect or spreading, sparsely woolly-pubescent, 10–15 cm long, very leafy towards the base: leaves all simple, crowded, glabrous or nearly so, linear-subulate, cuspidate, either appressed or spreading: flowers white, closely capitate, the heads large (10–20 mm in diameter): calyx lobes subulate, with a green midrib, a little shorter than the scarious tube: corolla tube 4–6 mm long, exceeding the calyx lobes, its oval lobes noticeably shorter than the tube: stamens exserted, the filaments a little shorter than the corolla lobes: capsule broadly oval, longer than the calyx tube, its cells 1-seeded.

In habit this species suggests *G. congesta* or *G. iberidifolia*, but the numerous short, simple leaves are wholly distinguishing even without the other characters. I name it for Mr. Elmer D. Merrill, who, in company with Mr. E. N. Wilcox, made an extensive and valuable collection in western Wyoming and eastern Idaho, in the summer of 1901. It was secured on dry soil, fifteen miles south of Leckie, Wyoming, June 15; no. 746.

Gilia Wilcoxii, n. sp.—Annual, 1–3 dm high, generally branched from the base; the branches in turn sparsely branched, erect or (if several) decumbent at base, somewhat floccose woolly, tardily glabrate: leaves less woolly than the stems, alternate, 2–5 cm long, pinnate; the segments narrowly linear, mucronate, the lateral ones widely divaricate, short (mostly less than 1 cm), usually two pairs: flowers in small bracteate clusters

terminating the branchlets, involved in wool especially the base of the calyx and the subtending green foliar bracts; bracts pinnately 3-cleft, the terminal lobe surpassing the calyx: sepals 5, green, equal or nearly so, pungently mucronate, hardly united except by the enveloping wool, about 7^{mm} long: corolla light blue, tubular, dilating into a broader throat, tube surpassing the calyx, lobes oblong, obtuse, about half as long as the tube: stamens scarcely exerted (the anthers only in the sinuses of the corolla lobes): ovules about four to each cell, not all maturing: seeds small, rhombic in outline, obscurely scarious on the angles and the tips, apparently not developing mucilage when wetted.

This is a close ally of *G. floccosa* Gray, which is a plant of Oregon, extending southwest into California. In this species it may be noted that the leaves are usually simple, the calyx of four unequal lobes, the corolla tube yellow, the anthers exerted, the seeds fewer, larger, not angled, developing copious mucilage.

Following Bentham, Mr. Howell in his *Fl. N. W. Am.* restores to generic rank the section HUGELIA and places in it *G. floccosa*. If that genus is to stand, the species now proposed must find its way into it, but I am unable to see any valid generic characters.

Named for Mr. Wilcox, mentioned above, who with Mr. Merrill secured three collections of it, all near St. Anthony, Idaho, in July 1901; nos. 822, 862, and 952.

Lappula columbiana, n. sp.—Annual, 3–5^{dm} high, hirsute with soft white hairs, those on the leaves with pustulate base: stem simple below, upward freely and divaricately branched; the branches tapering, long and slender, sparsely fruited: leaves from linear-spatulate (below) to linear, passing into the bracts which exceed the short pedicels: sepals nearly linear, 5–6^{mm} long, surpassing the fruit: corolla small, mostly light blue: nutlets similar, prickles few (7–9), united below into a shallow, involute-margined cup, finely and closely muricate ventrally, the murications on the dorsal face (disk) in about three rows, those of the middle row largest.

This is the *L. texana* of the *Flora of the Palouse Region* by Piper and Beattie; *Fl. N. W. Am.* Howell in part at least; not *L. texana* (Scheele) Britt. The latter is indeed Texan and not well known. Neither may it be considered *L. cupulata* (Gray) Rydb. (See Bull. Torr. Bot. Club 28: 31). Now

that the old and troublesome aggregate has been broken up, there is no way left except to constitute this a species. Its range seems to be in the region of the tributaries of the Columbia. Three collections are represented before me: no. 1703, C. V. Piper, Alamota, Wash.; A. A. & E. Gertrude Heller, Nez Perces co., Idaho; L. F. Henderson, Lewiston, Idaho.

Lappula cucullata, n. sp. — Sparingly cinereous-pubescent throughout: tap-root slender: several to many-stemmed from the crown, the stems simple or sparingly branched, only 1–2 dm high: leaves numerous, small, narrowly oblong, 1–3 cm long, passing into the small foliar bracts: nutlets similar, and all deeply cupulate or hooded, the border of the hood thin and strongly involute, the rounded margin bearing a few short glochidiate prickles, the tip of the nutlet with nearly an equal number of slender prickles not involved in the border of the hood (these characters not fully developed till maturity); the body of the nutlet with a dorsal slightly muriculate ridge, ventrally orbicular with an abrupt acumination, strongly keeled, the sides closely muriculate.

This has possibly its nearest ally in *L. heterosperma* Greene, but is somewhat differently branched, is less cinereous, and has the nutlets all alike.

The type number is 7250, Fort Steele, Carbon co., Wyo. Dry, sandy slopes.

LAPPULA HETEROSPERMA homosperma, n. var. — Larger than the species, paniculately branched from the base upward: nutlets all similar and with the characters of the cupulate ones of the species.

Specimens of the variety by Mr. G. E. Osterhout, New Windsor, Colo., June 23, 1899.

Cryptanthus depressa, n. sp. — A small depressed annual, freely and divaricately branched, 3–6 cm high and more widely spreading, the dense pubescence soft-hispid, white with a slight fulvousness in the inflorescence: leaves small, linear, 10–15 mm long: flowers minute: sepals linear, shorter than the corolla: corolla 2 mm long, its lobes less than half the length of the slender tube: anthers below the middle of the tube: nutlets ovate, acute, smooth, the linear scar nearly closed and forked at the base, more than 1 mm long.

It has the aspect of some of the species of the deserts of the southwestern United States, but I am unable to find a close ally.

Collected by Messrs. E. D. Merrill and E. N. Wilcox, dry soil, seven miles west of St. Anthony, Idaho, July 8, 1891; no. 873.

Cryptanthe Howellii, n. n.—*C. multicaulis* Howell, Fl. N. W. Am. 487; not *C. multicaulis* Aven Nelson, Bot. Gaz. 30: 194.—This species may appropriately be named for its discoverer and describer, the indefatigable student of our northwestern plants, Mr. Thomas Howell.

Oreocarya cana, n. sp.—The multicapital caudex tufted, its branches clothed at their summits with the densely pubescent leaf bases: stems single from the crowns, 1–2^{dm} high, simple, softly and closely pubescent: leaves silvery white with a short, close, soft pubescence; the numerous crown leaves linear-oblongate, 3–7^{cm} long, scarcely petioled; stem leaves shorter, sessile above: inflorescence a short dense thyrsoid spike, its pubescence moderately dense and slightly fulvous (scarcely hispid): sepals linear, 5–7^{mm} long: corolla white, its tube as long as the calyx: nutlets narrowly ovate, angled at the sides, densely muriculate on the back and sides, ridged on the back by a double row of minute tubercles, scar open lanceolate, about 3^{mm} long, rarely all maturing.

This plant was first collected in 1894, and now again from near the same locality in excellent flower and fruit. In habit it is intermediate between *O. suffruticosa* Greene and *O. caespitosa* Aven Nelson, but perhaps more nearly allied to the latter, from which it is at once separated by its silvery white foliage, its larger size, and muricate nutlets. No. 8309, collected on gravelly, open hilltops, Fort Laramie, Wyoming, is the type.

Mimulus membranaceus, n. sp.—A weak diffusely spreading annual, nearly glabrous throughout, but slightly clammy in the fresh state: stems slender, nearly prostrate, geniculate at the nodes, from a few centimeters to 1 or 2^{dm} long: leaves very thin, elliptic to broadly ovate, entire or crenate-dentate, on pedicels about equaling the blade: flowers in the axils, on filiform pedicels which are several times longer than the calyx: calyx tubular, obscurely glandular-pubescent, 2–3^{mm} long, the teeth small, much elongated, somewhat inflated and distinctly angled

in fruit: corolla yellow, very moderately bilabiate, nearly tubular, 5–8^{mm} long: capsule not stipitate, elliptic, obtuse, nearly equaling the slender style which barely protrudes from the mature calyx: seeds nearly oval, very small.

This is the counterpart in this range of *M. alsinoides* Benth. of the Washington-Oregon flora. From that species *M. membranaceus* differs principally in the enlarged and angled calyx, the scarcely bilabiate corolla (without the purple spot on the lip), and in the obtuse capsule and orbicular seeds.

Of the three collections of this all were secured in the Medicine bow mountains, always growing more or less in the shade of wet rock ledges and cliffs; nos. 1515 (1895); 1683 (1895), type; and 7729 (1900).

MIMULUS LEWISII tetonensis, n. var.—Smaller than the species in every way, more granular-glandular: calyx lobes shorter, narrowly linear-acuminate: corolla shorter, white or tinged with yellow.

Collected by Elmer D. Merrill and E. N. Wilcox in the Tetons, Wyoming, at 11,000 ft., near Lee's lake, July 26, 1901; no. 1072.

PENTSTEMON COMARRHENUS Gray—I wish to call attention to the distinctness of *P. comarrhenus* Gray (Proc. Am. Acad. 12: 81) and *P. strictus* Benth. (DC. Prod. 10: 324). *P. strictus* in Gray *Syn. Fl.* 2: 262 seems to include both, though probably referring mainly to the plant of Utah and western Colorado. *P. strictus* was founded upon immature specimens collected by Fremont on the Platte river in Wyoming, where it is abundant, though apparently not again collected until within the last few years, hence the confusion. Good specimens of the two species when compared leave no doubt as to the validity of both. Typical specimens of *P. strictus* are my nos. 1472, 1579, 3079, and others from Wyoming and adjacent Colorado. Of the other species Mr. M. E. Jones's no. 5484, Castle gate, Utah, seems to me to be typical. Mr. Baker's no. 604, Piedra, Colo., will also probably go here.

Pentstemon xylus,¹ n. n.—*P. caespitosus suffruticosus* Gray, Syn.

¹This description and the notes upon it were written before I discovered Dr. Rydberg's *Pentstemon suffrutescens*, Bull. Torr. Bot. Club 28: 503. From the very limited notes there given I judge that he and I are considering totally different plants. As I feel quite certain that I have the true *P. caespitosus suffruticosus* Gray, I still present this description. If I be right, Dr. Rydberg's *P. suffrutescens* is practically a *nomen nudum* until he presents a description of it.

Fl. 10: 270; not *P. suffruticosus* Dougl., Benth. in DC. 10: 330.—Caudex woody, its branches prostrate spreading: the annual herbaceous stems slender, erect, not crowded, sparsely leafy, finely puberulent, 1–2^{dm} high: leaves linear-oblongate to spatulate, acute or obtuse at apex, tapering very gradually to the slender base, 1–2^{cm} long, shorter than the internodes, nearly or quite glabrous: inflorescence open; the short peduncles at right angles to the stem, with about three short-pedicelled, nearly erect flowers: sepals nearly linear, sparsely glandular-pubescent, about 4^{mm} long: corolla moderately ventricose, with sub-equal lips, obscurely and sparsely glandular pubescent, a few long hairs in the throat: the sterile filament moderately bearded to its base.

The specimens before me were collected by Mr. H. N. Wheeler at Sapinero, Colo., 1898, no. 446, and in my judgment are referable to *P. caespitosus suffruticosus* Gray. As suggested by Dr. Gray, this seems to be a distinct species, though clearly related to *P. caespitosus*.

Pentstemon Owenii, n. sp.—Perennial from a much branched, cespitose, woody caudex, 1–2^{dm} high: stems numerous, erect from a more or less decumbent base, rather slender, glabrous, or with an obscure puberulence, most of them tinged with purple, some of them deeply so: leaves glabrous, numerous on the crowns of the caudex (many of the branches of the caudex terminating in short, slender, sterile, leafy shoots), narrowly elliptic (some of the earlier ones from obovate to spatulate), mostly acute at apex, 2–4^{cm} long, tapering cuneately at base into a petiole which is usually much shorter than the blade (rarely nearly equaling it); the stem-leaves several, the lower much like those of the crowns, becoming narrower and lanceolate upward, passing into the bracts of the inflorescence: thyrus crowded, from capitulum-form to short spicate and somewhat interrupted-verticillate, minutely glandular-pubescent especially on calyx and pedicels: sepals lanceolate, one-third as long as the corolla, the broadish base scarious margined, the green central portion continued into the acuminate tip: corolla violet-blue (or sometimes purplish?), tubular, but slightly dilated upward, 12–15^{mm} long, only

moderately bilabiate; the lobes entire, rounded, sparsely bearded on the lower lip: sterile filament but slightly enlarged upward, rather stiffly bearded at tip; anthers dehiscent through the junction of the cells, but not explanate.

That the large number of forms that have figured as *P. confertus* Dougl. and varieties of it have given rise to no little trouble is admitted by all. An aggregate is always confusing. As tending toward a simplification, it seemed to every one proper to restore to specific rank *P. procerus* Dougl., published by Graham in Edinb. Phil. Journ., 1829. This, so long known as *P. confertus caeruleo-purpureus*, is so evidently distinct that no one ever thinks of mistaking it for the species to which it has been appended.

The species now proposed, while a member of this same group, is as distinct from *P. procerus* as the latter is from *P. confertus*. The habitat of the two is characteristic. *P. procerus* is found at middle elevations and up to the limit of trees, occurring on moist slopes and in the valleys. *P. Owenii* is strictly alpine and occurs in clumps among the rocks of the "slides." The former is glabrous, the latter puberulent on the stems and glandular-pubescent on the inflorescence. The inflorescence of the former is nominally verticillastriform, of two to five rather remote verticils; the latter is spicate-capitellate with at most one proximate verticil, and the corollas of the latter are much larger than in the normal form of the other, less strongly bilabiate, and relatively longer when compared with the calyx.

This species is dedicated to that intrepid mountaineer, Hon. W. O. Owen, who in September 1898, with a small party, successfully scaled the Grand Teton and left upon its summit permanent record of the achievement. Mr. Owen brought back from this memorable trip several specimens of alpine plants, among which was a specimen of this species. It has been collected again in 1899, August 16, by the writer, this time also on the Tetons at an alpine station, no. 6515 being the type. More recently collected by Messrs. Merrill and Wilcox, 1901, and again on the Tetons.

Synthyris flavescens, n. sp.—Nearly glabrous throughout from the first, green even to the floral bracts: rhizome thick, short, horizontal, with numerous thick, fibrous roots: stems few to several, strict, leafy-bracteate, 3–5^{dm} high: leaves few, radical, ovate-lanceolate, sub-acute, finely serrate-crenate, 6–10^{cm} long, mostly exceeding the comparatively slender petioles; the foliar bracts of the stem broadly ovate, acute, serrations similar to those of the leaves, 1–2^{cm} long; floral bracts ovate-rhomboid to lanceolate, acute, entire or very unequally two-lobed, sessile

by a narrowed base, sparingly ciliate-margined as are also the sepals: spike dense, 5-10^{cm} long; the flowers short-pedicelcd: calyx unequally 4-cleft, the lobes elliptic, toothed at apex: corolla yellow or greenish-yellow, cleft at either side nearly to the base; the upper lip broadly obovate, with cuneate base and entire or toothed summit, exceeding the calyx and the 2-3-cleft lower lip by about half: stamens exserted, with purplish filaments and yellow anthers: mature fruits not at hand.

This species was collected and distributed by Professor C. S. Crandall as *S. plantaginea* Benth. To this it is allied, but more closely to *S. Ritteriana* Eastwood, though even from this it differs in many essential respects. Collected at Cimarron, Montrose co., Colo., May 18, 1898.

SYNTHYRIS RITTERIANA obtusa, n. var.—Leaves very obtuse, exceeding the scarcely margined petiole; foliar bracts suborbicular, usually cuspidate; floral bracts merely acute, distinctly purple-veined on the inside, with a narrowed base but not petioled: calyx parted to the base at the sides, the two lobes similar, orbicular or reniform, sometimes one or both from slightly to deeply cleft near one side, thus giving a 3 or 4-cleft calyx of unequal lobes: corollas yellowish-white, slightly exceeding the calyx, the two lips parted to the base; the upper lip rounded or truncate; the lower nearly similar or laciniately toothed or lobed.

If the above characters, which are mainly points of distinction between this plant and *S. Ritteriana*, are not specific, they at least call attention to a good variety. The specimens are those distributed by Messrs. Baker, Earle, and Tracy, no. 225, as *S. Ritteriana*, and bearing the note "this but a short distance from the type locality where it was also observed." In spite of the locality, the plant fails to measure up to the characters, and must be at least varietally distinct. In case the now proposed variety must later be included into the species, the description of the latter will have to be materially modified; but in the absence of the type specimen I leave it as a variety.

Gaertneria tomentosa (Nutt.), n. comb.—*Ambrosia tomentosa* Nutt. Gen. 2: 186. 1818; *Franseria discolor* Nutt., Trans. Am. Phil. Soc. n. ser. 7: 345. 1841; *Xanthidium discolor* Delpino, Studi sopra Artemis 62. 1871.—That Nuttall's *Franseria discolor* is simply his *Ambrosia tomentosa* seems more than probable. As

Dr. Gray states in the *Syn. Fl.*, "station and characters" indicate this. In the *Kew Index* this synonymy is accepted without question. Then, too, Nuttall's characterization, "leaves tomentose on the lower surface," would imply that the upper surface was not tomentose. It is true also that while Dr. Gray in *Pl. Fendl.* thought his *Franseria tomentosa* was Nuttall's *Ambrosia tomentosa*, he changed his mind about the matter in a later publication (*Syn. Fl.* 251).

Gaertneria Grayi, n. nom.—*Franseria tomentosa* Gray, *Pl. Fendl.* 80.—Since the preceding change necessitates another, this species may appropriately be dedicated to the original describer.

UNIVERSITY OF WYOMING,
Laramie, Wyoming.

THREE NEW GENERA OF THE HIGHER FUNGI.

GEO. F. ATKINSON.

(WITH THREE FIGURES)

I. EOMYCENELLA, A NEW GENUS OF HYMENOMYCETES.

THIS interesting plant was found during September 1899, on fallen leaves of *Rhododendron maximum* at Blowing rock, N. C. The plant is very minute, entirely white, possesses a delicate pileus which is broadly campanulate or depressed in age, and a very slender, fleshy stem. An examination with the hand lens showed that there were no lamellae, the underside of the pileus being plane. The *Rhododendron* leaves, partly dry, rolled in such a way as to protect the fungus, and in this condition it was shipped to Ithaca. On examination with a higher power microscope, it was found that the hymenium had dissolved so that the spores lay against the underside of the framework of the pileus in the amorphous layer of dissolved tissue. From this material it was clearly impossible to determine the structure of the fungus. The leaves were then placed in a moist chamber, and in the course of a few days a new plant appeared, and for some time successive ones grew and I was enabled to study the structure.

For some time none of the plants showed any trace of lamellae, and it appeared that the fungus belonged to the Thelephoraceae. but later one plant was grown somewhat larger than the others, which had rudimentary lamellae, eight of a larger size and four very small. This at once opens the question as to whether the plant belongs to the Thelephoraceae or to the Agaricaceae and whether originally the hymenial surface was plane, and the form with lamellae represents a later stage in the evolution of the plant; or whether the gill form represents the original character of the species, which by reduction loses its lamellae. The latter condition is seen sometimes in *Marasmius epiphyllus* Fr.,¹ and I have

¹ PERSEON, *Icones pl. g. fig. 7.*; STEVENSON, *Brit. Fung., Hymen. 2: 152.*

seen specimens of *Lepiota procera* in which large areas on the under side of the pileus were destitute of lamellae. The additional characters of the fungus are to be found in the following description:

EOMYCENELLA Atkinson, n. gen.—Plants stipitate. Pileus campanulate to expanded, consisting of a layer of radiating branched threads forming a more or less lattice-like or trabecular, expanded, thin structure; trama wanting or very rudimentary the subhymenium arising directly from the trabeculae of the pileus. Hymenium plane, or in larger forms with a few short, narrow, distant lamellae not reaching the stipe; lamellae with rudimentary trama. Basidia clavate, 4-spored. Spores smooth, 1-celled, hyaline. Stipe fleshy, delicate. At maturity hymenium dissolving, leaving many of the spores lying on an amorphous layer against the trabeculae.—One species, on decaying leaves of *Rhododendron maximum*, Blowing rock, N. C.

Eomycenella echinocephala Atkinson, n. sp. (fig. 1).—Plants white, 3–8 mm high. Pileus 0.5–0.75 mm broad. Stipe 60–80 μ in diameter. Plants campanulate to expanded and upturned in age, trabeculae of upper surface echinulate, bearing here and there

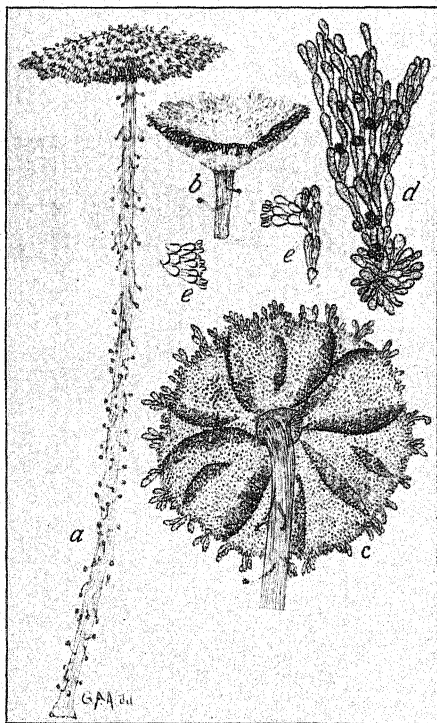


FIG. 1.—*Eomycenella echinocephala*: a, entire plant; b, pileus in older stage; c, under side of pileus, showing rudimentary gills in larger plant; d, detail of trabeculae of pileus; e, detail of basidia and spores.

globose free branches, $10-15\mu$ in diameter and also echinulate, margin of pileus with free clavate branches in the form of a fringe. Cells of the trabeculae $25-30 \times 6-10\mu$. Hymenium plane or with few short, narrow gills. Gills when present narrowed at each end, not reaching the stipe. In the plant observed 8-10 long lamellae, 4-6 intermediate ones much shorter. Subhymenium loosely branched, obovate cells arising from the trabeculae and terminating in the basidia, or in the forms with lamellae arising from a rudimentary trama in the lamella. Basidia short clavate, abruptly narrowed into a pedicel, $9-12 \times 6-9\mu$, 4-spored. Spores obovate-oblong, elliptical, proximal end pointed, $6-8 \times 3-4\mu$, hyaline, smooth, granular. Stipe thread-like, with scattered hairs bearing a short echinulate cell on the end. Base of stipe only slightly broadened.

Eomycenella is related to *Discocyphella*² P. Hennings, but differs in the dissolving hymenium and the fact that the pileus is not gelatinous nor the stem horny. From *Cymatella*³ Patouillard (placed with Agaricaceae) it differs in the trabecular pileus and the dissolving hymenium; and from *Gloecephala*⁴ (Clavariaceae) Massee, which has one-spored basidia. The latter should be placed in the Thelephoraceae.

II. EOTERFEZIA, THE TYPE OF A NEW GENUS AND FAMILY OF ELAPHOMYCETES.

This fungus appeared as a parasite on *Sordaria* grown in the laboratory in the spring of 1897. Cow dung which had been lying on the ground all winter was collected early in the spring of 1897 in a pasture field just beyond Buttermilk creek, near Ithaca, N. Y. This was placed in a moist chamber and in the course of a few weeks the *Sordaria* made its appearance. The species of *Sordaria* was not determined. After the cultures had been kept a week or so longer, there appeared on the perithecia of *Sordaria* minute white, knot-like protuberances which were smaller than the perithecia and stood out in strong contrast to the dark brown wall of the host. These minute bodies, subglobose or kidney shaped, were nearly smooth, possessing a few scattering free threads arising from the surface, and their texture was soft and fleshy.

²ENGLER and PRANTL, Pflanzenfamilien 1²: 554. ³*Ibid.* p. 555. ⁴*Ibid.* p. 131.

On examination of the structure it was at once clear that the fungus was a very interesting one. Nearly the entire interior of the fruit body is occupied by minute asci, not collected into a single tuft as in the pyrenomycetes, but scattered and intermingled with the mycelium. The asci are separated into small fields by radiating strands or thin plates of mycelium, forming sterile avenues from which the branches arise that ultimately bear the asci and are intermingled with them. Since the fields of asci are more or less elongate and thin, they too, have a more or less radial direction from the point where the fruit body is in contact with the host. The surface of the fruit body is a thin and delicate wall formed by the coalescence of hyphae into a membranous envelop which is joined by the terminations of the radiating sterile avenues.

The arrangement of the asci in fields separated by sterile avenues of mycelium suggested that the fungus was related to the Tuberineae. However, the asci do not form a hymenium lining the walls of chambers in the interior, but they are irregularly intermingled in the fields which they occupy. This places the fungus definitely in the order Plectascineae.⁵ In Fischer's arrangement of this order there are six families. In the first three families, Gymnoascaceae, Aspergillaceae, and Onygenaceae, the asci are irregularly distributed throughout the interior of the fruit body, while in the Elaphomycetaceae and Terfeziaceae⁶ there are sterile avenues separating the fertile fields into groups. It is evident that our plant possesses certain points of close agreement with these two families, but the internal structure is much more simple, and the asci and spores are not so highly specialized, while the thin membranous, rudimentary envelop is very unlike the thick and differentiated wall of the members of these two families.

It is evidently a plant of very simple structure. It shows some points of resemblance in this respect with the Gymnoasca-

⁵ ENGLER and PRANTL, *Pflanzenfamilien* 1¹: 290.

⁶ The Trichocomaceae have a highly specialized and peculiar capillitium, too remote from our plant for comparison.

ceae; but, as stated above, the differentiation of the interior into sterile avenues and fertile fields does not admit of its location in that family. Furthermore, the envelop of the fruit body in the Gymnoascaceae is arachnoid, while the envelop of our plant, though simple and very thin, is membranaceous. It represents

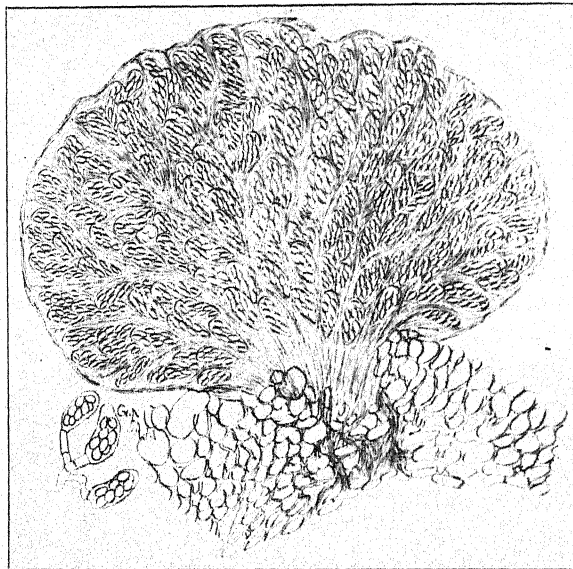


FIG. 2. *Eoterfezia parasitica*, showing section of fruit body and portion of perithecial wall of *Sordaria*.

not only a new generic type, but also the type of a new family. These may be characterized as follows:

EOTERFEZIACEAE Atkinson, n. fam.—Fruit bodies with a thin but distinct wall of closely interlaced hyphae. Interior with sterile avenues connected with the wall and separating the fertile areas where the asci are irregularly arranged.

EOTERFEZIA Atkinson, n. gen.—Fruit bodies subglobose, minute, fleshy, with a distinct but very thin, undifferentiated wall, smooth or slightly hairy. Interior of fruit body with sterile avenues radiating from the base and branching until they unite with the wall. Fertile areas lying between containing the asci

intermingled with the supporting hyphae. Spores smooth, hyaline, one-celled. Interior not disintegrating into a powdery mass at maturity. At present one species as follows:

Eoterfezia parasitica Atkinson, n. sp.—Fruit bodies subglobose to kidney shaped, white, fleshy, $100-300 \times 100-200 \mu$, sessile, closely attached to the perithecia of the host, the mycelium issuing from the inside of the perithecium in a broad, stout strand, and then radiating. Wall of the fruit body distinct and well differentiated, but very thin ($3-5 \mu$), membranaceous, and undifferentiated, with here and there rather long free branches of mycelium, but not distinctly hairy. Sterile avenues radiating from the point of attachment with the host, and branching as they approach the periphery, thin, but distinct, and separating the fertile areas into thin plates in which the asci are intermingled with the hyphae. Asci elliptical-oblong, $15-20 \times 8-10 \mu$. Spores elliptical-oblong, smooth, $3-3.5 \times 1.5-2 \mu$, biserial.—Parasitic on perithecia of a *Sordaria*, Ithaca, N. Y.

It might be as well to consider the position which the *Eoterfeziaceae* occupy in relation to the other families of the *Plectascineae*. When I first discovered the plant, I was impressed with the resemblance of the asci and spores to those of *Ascocorticium* of the *Protodiscineae*, and those of some species of *Endomyces* of the *Protoascineae*. It is probably more nearly related to the latter. But the *Gymnoascaceae*, especially the genus *Arachnietus*, show very close relationship to *Endomyces*, both in the arachnoid envelop and in the undifferentiated condition of the fertile portion. *Eoterfezia* is perhaps an offshoot from such a plant as *Arachnietus*. The relationship of the families might be suggested by the following scheme:

Gymnoascaceae - -	{	Aspergillaceae - -	(? Erysiphaceae).
		- - - -	? Onygenaceae.
		- - - -	? Trichocomaceae.
		Eoterfeziaceae - -	{ Elaphomycetaceae. Terfeziaceae.

KEY TO THE GENERA OF PLECTASCINEAE.

Interior of fruit body undifferentiated,				
Wall of fruit body arachnoid, simple	-	-	-	<i>Gymnoascaceae</i>
Wall of the fruit body firm, thick,				
Fruit bodies not stalked	-	-	-	<i>Aspergillaceae</i>
Fruit bodies stalked	-	-	-	<i>Onygenaceae</i>

Interior of fruit body differentiated,		
Wall of fruit body very thin, membranaceous	- -	<i>Eoterfeziaceae</i>
Wall of fruit body stout,		
Spore mass powdery	- - - - -	<i>Elaphomycetaceae</i>
Spore mass not powdery	- - - - -	<i>Terfeziaceae</i>
Interior of fruit body with a highly specialized capillitium		<i>Trichocomaceae</i>

III. DICTYBOLE, A NEW GENUS OF PHALLOIDS.

This plant was collected by W. H. Long, Jr., at Denton, Texas, Oct. 15, 1901. It is peculiar and striking in that it possesses a dimorphic gleba, the upper part of which is traversed by sterile, radiating, imbricate plates suggesting the gleba of *Itajahya*, while the lower part of the gleba is latticed something after the fashion of *Simblum*. From the gross characters of the gleba it would seem to occupy an intermediate position between the two genera, the former being placed by Fischer in the Phallaceae, while the latter is a member of the Clathraceae. However, in *Itajahya* the sterile plates are pseudoparenchymatous, while in *Dictybole* they are floccose, and *Dictybole* therefore belongs in the Clathraceae.

The upper part of the volva in the specimens seen remains adherent to the pileus, so that in the elongation of the receptacle the volva ruptures in a circumscissile manner, leaving the edge of the pileus more or less irregularly lobed and pendent around the upper part of the receptacle, though sometimes the volva ruptures so high up that there is no free portion projecting. As the plant ages, the latticed portion of the gleba loosens from the stipe, except at the junction with the upper part of the pileus, and expands in such a manner as to form a pendent, loose, open, large meshed irregular network, which becomes easily torn asunder in several places. The plant when fresh has a peculiar, but pleasant and strong "amyl-acetate" odor. It represents the type of a new genus⁷, which may be characterized as follows:

DICTYBOLE Atkinson, n. gen.—Receptacle a hollow stalk with a chambered wall bearing at the apex a weakly devel-

⁷ Dr. Ed. Fischer, to whom the plant was submitted, confirms my opinion that it represents a new genus.

oped pileus covered by the gleba. Gleba dimorphic, the apical portion traversed by numerous sterile, short, radiating plates; the lower portion with convoluted folds in the form of irregular rings giving a latticed appearance to this portion of the gleba. At maturity the folds of the latticed portion of the gleba uncoil more or less and form long, irregular, loose, netlike folds. Spores single celled, smooth.—One species, Denton, Texas.

Dictybole texensis Atkinson & Long, n. sp.—Plants subterranean, emerging by the elongation of the receptacle, 7–10^{cm} high. Receptacle nearly cylindrical, slightly tapering downward, cream white, firm; pileus not perforated at the apex, usually pendent from apex of receptacle, and upper part of volva often in contact. Gleba at first drab, then black; sterile plates in upper part of gleba numerous, short, and narrow, arranged in a more or less radiating and imbricated manner; latticed portion with large oblong rings (8–16?), the surface rugose, and in age loosening out into a large open, irregular mesh. Spore bearing tissue between the sterile plates and lying between and over the lattice work. Spores pale olive brown, irregularly oval, $3-4 \times 2-3 \mu$, smooth. Volva large, white, circumscissile, rooting at the base. The plant when fresh has a pleasant but strong “amyl-acetate” odor.—In sandy soil. Denton, Texas.

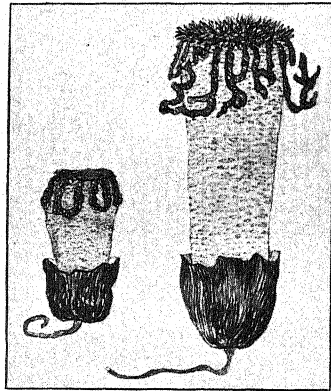


FIG. 3.—*Dictybole texensis*.

NOTES ON THE PHYLOGENY OF LIRIODENDRON

EDWARD W. BERRY.

(WITH ONE FIGURE)

THERE are many reasons why the tulip tree is an object of unusual interest, but its scientific interest chiefly arises from the facts that, like the Sequoia, Sassafras, Platanus, Ginkgo, etc., it is the lone survivor of an ancient race extending back into the Cretaceous period, that most of the race history can be traced, and that we find this history epitomized in the existing species.

Liriodendron Tulipifera is confined to the eastern portions of North America and Asia, although it or its probably identical representatives were common in Europe during the Tertiary period. Like other trees peculiar to North America at the present time, such as Magnolia, Liquidambar, Sassafras, etc., and which inhabited Europe during the Tertiary, it was forced to the Mediterranean by the glaciers and exterminated. The existing Asiatic form has been described as a variety (*chinensis*¹), but it is very doubtful whether it is distinct. In North America the tulip tree is found from Vermont to Florida and westward to Michigan and Arkansas, and appears to be confined to the humid temperate realm, requiring a rich soil for its full development.

The great variability among the leaves of the tulip tree, as well as the resemblance of some of them to fossil species, has attracted very little attention, possibly, as Holm suggests,² because this variability is so well known as not to merit discussion. The belief that this is not the case has led to the following notes, extending over a number of years, and based upon innumerable specimens. While these notes are incomplete and

¹ Descriptions of some new phanerogams collected by Dr. Shearer in China, etc., Jour. Bot. 13:225. 1875.

Enumeration of all plants known from China, etc. F. B. Forbes and W. B. Hemsley. Jour. Linn. Soc. 23:25. 1886.

² Proc. U. S. Nat. Mus. 13:15-35. 1890; Bot. Gaz. 20:312. 1895.

disconnected in many ways, it has seemed best to arrange and present them.

A common error is the belief that a truncate or emarginate apex is a constant feature, induced, no doubt, by a consideration of the vernation, which would seem to preclude any other form of apex, and which has been the subject of papers by Lubbock³ and others. Lesquereux⁴ says "leaves always truncate or emarginate at the apex," and Newberry⁵ makes the same statement. Holm,⁶ in his paper on the leaves of *Liriodendron*, goes still further, and insists that the notched apex is the true test of the genus *Liriodendron*, and hence unnotched leaves or forms with the apex of the leaf missing cannot be identified with certainty; and Hollick⁷ makes the statement that the apex is always cuneate or notched. Doubtless others have followed the lead of these authorities.

I have collected numerous leaves of *Liriodendron Tulipifera* with pointed tips, and I have also a number of similar specimens collected by Mrs. W. A. Kellerman, of Columbus, O., showing how fallacious the above cited criterion proves. Among my collections of these anomalous forms may be noted a simple obovate leaf closely resembling *Phyllites obcordatus* Heer; a trilobed form identical with *Liriodendron semialatum* Lesq. of the Dakota group; a small leaf unlike anything before known in this genus and almost exactly corresponding with *Cissites acuminatus* Lesq., pl. 5, fig. 3, of his *Cretaceous and Tertiary Floras*; a large trilobed leaf which is also a new form in the genus and recalls Heer's *Aralia groenlandica*; also numerous ovate-lanceolate leaf blades on leaf bearing flower buds (see fig. 3). The foregoing examples are sufficient to refute the claim that the notched apex is an essential character, and we should expect to find just such leaf forms if we accept the origin of *Liriodendron* from forms with simple, magnolia-like leaves. Fossil species based on leaf forms

³ Phytobiological observations. Jour Linn. Soc. 22: 24. 1887; and GODRON, A., Obs. sur les bourgeons et sur les feuilles des *Liriodendron Tulipifera*. Bull. Soc. Bot. France 8: 1861.

⁴ Flora of Dakota group, p. 229.

⁶ Proc. U. S. Nat. Mus. 13: 1890.

⁵ Flora of the Amboy clays.

⁷ Proc. Nat. Sci. Ass. Staten Is. 5: no. 7. 1896.

alone are always more or less problematical, and yet in many cases form alone has served for specific distinction.

Venation also is much depended upon in defining species, although both venation and leaf form are characters which vary in a marked degree in the modern tree, even on the same individual. Leaving out the anomalous forms from shoots, forced buds, saplings, etc., almost any sassafras or tulip tree will show a more or less wide variation among mature leaves on branches which theoretically (*i. e.*, fruiting branches) should bear typical leaves; and when we compare a series from different trees or of different ages the variation in shape and minor characters of venation is almost endless. Perhaps no style of venation is more characteristic generically than the peculiar form that obtains in *Liriodendron*. That it cannot be relied upon for specific distinctions we know from its wide variation on the living tree, as well as among the fossil species referred to this genus. In some specimens the secondaries are opposite instead of irregularly alternate; in some they are parallel almost to the margin and ascending; while in others they soon divide. The angles of divergence of the secondaries show every degree of divergence, acute angles, right angles, or obtuse angles. All that should be claimed for venation characters, generally speaking, is usefulness in generic distinction or as supplementary evidence in connection with species.

Holm considers nearly all of the described forms of *Liriodendron* invalid, while most authorities consider nearly all of them perfectly good species. Professor Ward's dictum, that for geological purposes it is not so much a question of correct botanical determination as the correct recognition of a plant once named and associated with a given deposit, is quite true; but it loses its force when we are considering forms with variable leaves, unless each variety is constant and peculiar to a given formation, which is obviously not the case. In pursuing the comparison through the intermediate forms of ancient *Liriodendrons*, who can say where to break the chain of gradations for the boundary of separate species; among the gradual modifications of form, strikingly similar to

a series of leaves of *Liriodendron Tulipifera*, who can say where *L. simplex* ends and *L. primaevum* or *L. Meekii* begins, or where *L. primaevum* ends and *L. semialatum* begins? The same variability and interrelation is shown among the leaves variously referred to *Aralia*, *Sterculia*, *Cissites*, *Menispermities*, *Protophyllum*, *Platanus*, *Sassafras*, etc.; and, while it may be argued that we should expect just such variable and intermediate leaves at a time when the flora of the globe was becoming rapidly differentiated, the argument loses force when we turn to a similar variability and interrelation of the modern forms of the same genera, when their leaves alone are considered.

In considering the thirty or more species and varieties of fossil forms ascribed to *Liriodendron* and its allies *Liriodendropsis* and *Liriophyllum*, we may distinguish them as all good species, or as three or four, or we may identify most of them with the modern form, dependent upon our conception of the term species. If the Cretaceous period, at the time the Dakota strata were being laid down, was the time of maximum development and diversification of the dicotyledons, it is difficult to understand how so many of the types are still persistent with all their essential characters unchanged (*Myrica*, *Betula*, *Quercus*, *Populus*, *Viburnum*, *Salix*, etc., and representatives of nearly all of the natural orders), even in some cases to specifically similar forms (as *Magnolia acuminata* and *M. tripetala*). If there was such a diversification of species at that time as we are led to believe, it is strange that most of the types persist comparatively unaltered through the later formations to the present time, instead of losing their character in further continued variation.

We have listed as follows a few of the reasons for considering some or all of the described species of *Liriodendron* invalid:

1. Their remains are more or less fragmentary, and therefore not determinable with certainty.
2. The shape and venation of leaves are poor specific characters at best.
3. A series of leaves of *Liriodendron Tulipifera* can be found which parallels the fossil species in both shape and size.

4. There is a close intergradation among the various fossil forms.

5. The more unusual fossil forms are mostly small leaves, and it is among the smaller leaves on shoots and saplings of *Liriodendron Tulipifera* that we find the most diverse shapes, and those forms which most resemble the diverse fossil forms.

6. The remains of different fossil species would be unlikely to occur associated with each other.

7. *Liriodendron* is a monotypic genus at the present time.

8. The existing tulip tree very probably extends back into the Tertiary period, there being no great climatic change except during the Glacial period, which was survived by all of our existing arboreal vegetation. It is not stretching a point, therefore, to assume that our existing species of *Liriodendron* might extend still farther back into the Cretaceous; other plants do (*Magnolia*), and paleontology affords many examples of such persistent animal types.

9. Nearly all of the fossil forms of *Liriodendron*, if found at the present time, would be unhesitatingly referred to *L. Tulipifera* from a consideration of their leaf form alone; and practically all of the abnormal leaf forms of *L. Tulipifera*, if found as fossils, would be considered distinct species.

10. If we assume that in the ancient forms of *Liriodendron* the largest and best developed trees were on hillsides, as is the case in the modern tree, then the smaller, more aberrant forms, which occur on vigorous saplings and shoots, inhabiting the more marshy situations, would be the forms mostly likely to become fossil.

11. A warm, humid climate during the Cretaceous might account for the variety in shape and size of the leaves, just as in *L. Tulipifera* the best nourished individuals are the most variable.

12. The fact that so many of the fossil forms were contemporaneous militates against considering them as different stages in the development of the genus. We might with equal propriety consider the existing varieties as actual stages.

13. The barren record of the Tertiary period would seem to

imply that the diverse forms are found in the Cretaceous simply because the conditions were favorable for the fossilization of the abnormal forms.

In opposition to the foregoing, our reasons for considering the various described species valid are:

1. The majority of abnormal leaf forms in the living *L. Tulipifera* are young leaves, and they would not be likely to become detached and preserved as fossils.

2. We have every reason to expect numerous species in a tree ranging over so many lands (Europe, Asia, America), and throughout such a long period of time (Lower Cretaceous to the present).

3. The Cretaceous was a period of development and variation in the dicotyledons.

4. Ontogeny, or the individual development of modern types, more or less parallels their phylogeny, or actual ancestry. Generally speaking, this applies to all animals and plants.

5. The weight of authority is all on the side of many species, Lesquereux⁸ going so far as to say "from the remarkable diversity of characters seen in the leaves of *Liriodendron* described in this volume, I believe that no botanist would be disposed to consider them as mere varieties of the original obovate simple leaves." In criticising Holm's paper on *Liriodendron*, Professor Lester F. Ward⁹ says "modern forms more likely represent the phylogenetic stages through which the present living species has passed." This is the view held by all, so far as I know, of the various authors who have written of this group, as Newberry, Lesquereux, Hollick, etc., in this country, and Heer, Ettingshausen, Unger, Saporta, Velenovsky, Massalonga, etc., abroad.

6. If stipules were present—and they must have been, since *Liriophyllum populoides* of the Dakota and *Liriodendron alatum* of the Laramie show their incipient stages—they should occur as fossils, either separately, if we assume them to have been fugacious, as they are at the present time, or attached to the petioles of the fossil leaves, if they were persistent.

⁸ Flora of Dakota group, pp. 205, 206.

⁹ Am. Jour. Sci. III. 40: 422. 1890.

In reply to the question whether each one of the described species of *Liriodendron* represents a definite species established in nature, we are compelled to answer in the negative; for the evidence that the majority of these forms were distinct species, in any proper sense, is entirely insufficient. At the same time, we are led to believe, from a study of these fossil forms in conjunction with the modern form and its varieties, that *Liriodendron* in the course of its evolution has passed through a series of parallel stages, as we will endeavor to show. It matters little whether we call these stages species or stages.

The purpose of Holm's¹⁰ paper on *Liriodendron* is stated as follows: "The object of these notes . . . is to prove that, as far as is known to the writer, there is not a greater difference in the foliage between many of the extinct species of *Liriodendron* than between a series of leaves from a very young tree or from a branch of an older one of our living *L. Tulipifera*;" and he then proceeds to attack the validity of the various species. Since 1890 a host of specimens, including many interesting forms,¹¹ have come to light, and much new material has been published. Two works in particular may be mentioned, the last labors of the pioneers Lesquereux¹² and Newberry¹³ being issued posthumously, as well as various contributions from Hollick and others on the plant remains from Long and Staten islands and elsewhere. The time seems opportune for recording some additional notes, and correcting several current inaccuracies. It is far from the purpose to attempt to diminish or increase

¹⁰ Proc. U. S. Nat. Mus. 13: 16. 1890.

¹¹ The following new species: *Liriodendropsis angustifolia* Newb., *l. c.*, p. 84; *Liriodendron alatum* Newb., Hollick in Bull. Torr. Bot. Club 21: 467. 1894; *L. acuminatum bilobatum* Lesq., *l. c.*, p. 207; *L. Snovii* Lesq., *l. c.*, p. 209; *L. succedens* Dawson, Trans. Roy. Soc. Canada 11: 62, pl. 8, fig. 26. 1893 (1894); *L. praetulipiferum* Dawson, *l. c.* fig. 27; and the winged petiole forms of *Liriophyllum populoides* Lesq., Hollick, *l. c.*

¹² Flora of Dakota group, edited by F. H. Knowlton. Monograph 17 U. S. Geol. Surv. 1891.

¹³ Flora of the Amboy clays, edited by Arthur Hollick. Monograph 26 U. S. Geol. Surv. 1895.

the number of described forms of *Liriodendron*, and so needlessly encumber the synonymy.

In comparing the ancient types of *Liriodendron* with the modern varieties of *L. Tulipifera*, the purpose is to establish the fact that those ancient forms of leaves which were simple, or with unnotched apices, or with winged petioles, and which some authorities are inclined to exclude from *Liriodendron*, are undoubtedly correctly identified as primitive forms of that genus.

THE EVOLUTION OF LIRIODENDRON.

Following Holm, we would consider the primitive ancestral type of *Liriodendron* to have been a simple, Magnolia-like leaf; for not only do all the modern relatives of *Liriodendron* have such leaves (*Magnolia*, *Anonaceae*, etc.), but there is a progressive simplification and reduction in lobation as we proceed back in time, the most primitive known forms having ovate or oblong simple leaves (*fig. 3*). We find in the growth of our modern *L. Tulipifera* a parallel development, from the youngest entire or merely notched forms to those of the mature, typically lobed leaves.

Generally speaking, no significance can be attached to the form of the cotyledons; but in this case they represent almost exactly the form we imagine to have been assumed by the primitive *Liriodendron* leaf, which grew in the early Cretaceous or Jura-Cretaceous. (See *Torreya* 2: *pl. 1. figs. 6-8*. 1902.) We picture this ancestor as a tree with simple, ovate or lanceolate leaves, short petioled and without stipules or bud-scales. The vernation of the leaves was probably conduplicate, as in the existing *Magnolia*, it being obviously improbable for it to have been reflexed in the ancestor of short-petioled leaves such as those of *Liriodendron simplex* and *L. primaevum*. We consider that this entire, oblong form of leaf, tapering at both ends to a blunt point, was succeeded by a series of forms ranging from *Liriodendropsis angustifolia* Newb. at the one extreme, through *Liriodendron simplex* Newb., *L. primaevum*

Newb., and *L. Meekii* Heer, to *L. semialatum* Lesq. at the other.

This more or less closely related group includes four types of leaves. The first, a narrow elongated leaf, with an emarginate apex (*Liriodendropsis angustifolia*), occurs in such numbers in the Amboy clays and is so uniform in shape as to warrant its consideration as at least a permanent variety, which developed from the simple lanceolate ancestral form by a reduction of the apex until it became emarginate in the Lower Cretaceous. The second type includes certain leaves which have been referred to *L. simplex*, and which resemble the preceding in outline, but are somewhat broader. They would have been developed easily from *Liriodendropsis angustifolia* by a slight shortening and broadening of the blade of the latter; and like it, this form is found in the Amboy clays. If we compare some of the figures of *L. simplex* with Lesquereux's *Myrsine crassa*,¹⁴ they seem to be identical.

The third type of leaf is connected with the preceding by insensible gradations from the elongated emarginate forms, showing a constantly increasing width of blade, together with a shortening of its length, the emarginate apex becoming less and less so, until it is simply retuse. If these leaves were somewhat shortened and broadened, they would be identical with the usual form of young leaves of *L. Tulipifera*. If *Phyllites orbicularis* Newb. (Flora Amboy clays, 136. pl. 24. figs. 7, 8) be compared with young leaves of *L. Tulipifera*, they seem very similar and possibly identical. The various fossil leaves referred to *Colutea primordialis* Heer are also of this type, and the same may be said of *Sapotacites retusus* Heer.¹⁵ The resemblance of these ancient *Liriodendron* leaves to various leaflets of existing Leguminosae has also been noted by several authors. We have found many specimens of *L. Tulipifera* leaves that belong here, which shows conclusively that these ancient leaves are true *Liriodendron* leaves. This type is represented by various fossil

¹⁴ Flora Dakota group, pl. 52. figs. 2, 3.

¹⁵ See Flora of Amboy clays, pl. 53. figs. 5, 6.

forms referred to *L. simplex* and *L. primaevum* Newb., showing every gradation in form from the elongated notched leaves through the typical *L. simplex* to the broad forms of *L. primaevum*, which show a tendency to develop four lobes, a stage reached in *L. Meekii* Heer. The typical forms of *L. primaevum* are later in point of time than *L. simplex*, being found in the Dakota group, which forms the lowermost layers of the Upper Cretaceous; while *L. simplex* begins in the Amboy clays, long thought to be the same age as the Dakota, but now referred to some of the later Potomac series (Albirupear) of the Lower Cretaceous. However, many of the forms which have been referred to *L. simplex* are intermediate between it and *L. primaevum*, there being no very clear lines of demarkation among *Liriodendropsis angustifolia*, *Liriodendron simplex*, *L. primaevum*, and *L. Meekii*; each being a modification of the preceding through insensible gradations. It is but a step from some forms of *L. primaevum* to *L. Meekii*, and we have among our collections of *L. Tulipifera* many leaves that approximate those of *L. Meekii* in shape.

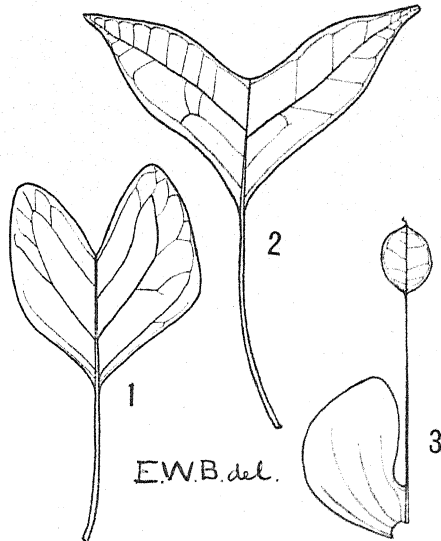
The fourth type of this group represents the other extreme of form, and is somewhat removed from the preceding three. It preserves the pointed apex of the original ancestor, which gradually broadened until it developed an obtuse basal lobe on each side. This form is represented among our known fossil forms by *Liriodendron semialatum* Lesq., and among leaves of *L. Tulipifera* by several specimens. *L. semialatum* is found in the Dakota group, and would have had ample time to develop into a broader leaf with basal lobes during the long period of the Lower Cretaceous when the Amboy clays were being deposited along our eastern coast. The small leaves from the Upper Cretaceous of Vancouver island, described by Dawson as *L. succedens*, if they belong to this genus would be the natural descendants of *L. semialatum*.

If we call the theoretical oblong-lanceolate form *stage 1*, the preceding five closely related leaf types fall naturally in a group which may be called *stage 2*.

Somewhat aside from the preceding are those forms included in *Liriophyllum*, a genus established by Lesquereux in 1876¹⁶ to contain certain leaves from the Dakota formation evidently allied to *Liriodendron*. They are somewhat coriaceous in texture, with obscure venation, and differ widely in outline from any known forms of *Liriodendron*, being (except *L. obcordatum*, which is probably not a *Liriophyllum* at all) square or broadly rhomboidal in general outline, and split at the apex along the line of the midrib about half way to the base, the two lobes being sublobate or bilobate, and separated by an obtuse sinus. Just what is the relation between these leaves and *Liriodendron* is hard to say. We know of no forms of *Liriodendron*, either ancient or modern, that approach very closely the peculiar shapes of *Liriophyllum populoides*, and *L. Beckwithii*. Fig. 1 shows the nearest form to *Liriophyllum* I have been able to find in some ten years collecting. In no case, however, is the resemblance very close, the nearest being those which would be identical with *Liriophyllum populoides* were the base somewhat wider. Bilobate leaves with a deep, wide sinus at the apex are common enough, the leaves tending to assume that form in the vicinity of flowers, or where the nourishment is defective; but none of them show any tendency to widen at the base, or contract the width of the sinus as in the leaves of *Liriophyllum* (fig. 2). There are two forms of *Liriodendron* leaves, either of which I conceive could have been ancestral to *Liriophyllum*. One is the common form of young leaves on modern shoots, and needs but to become parted farther down along the midrib, and to more largely develop the basal and apical lobes, to be a true *Liriophyllum*. The other is some form similar to *Liriodendropsis angustifolia*, which, by a shortening and widening of the blade, through some such form as *Liriodendron alatum*, might lead to *Liriophyllum*. Of the two, the latter seems to be the more tenable, for the orbicular notched leaves, first mentioned above, have never been found in the fossil state, unless *Phyllites orbicularis* may be so considered. It requires but a slight enlargement

¹⁶ Hayden's U. S. Geol. and Geog. Survey, p. 482.

of *Liriodendropsis angustifolia* to secure a form similar to *Liriodendron alatum*, and by a slight shortening and broadening of the blade in the latter we obtain a form from which it is an easy transition to *Liriophyllum populoides*, through forms with slightly more ascending apical lobes, and with a greater development of the basal portion of the blade in a lateral direction. I would consider *Liriophyllum obcordatum* as co-laterally descended from some simple ovate form such as some of the forms referred to *Liriodendron primaevum*. In either case, a lengthening of the next to the last pair of primaries, and the resulting lobes, would give a form identical with *Liriophyllum obcordatum*. However, we do not consider this a true species of *Liriophyllum*; it is either a young and anomalous *Liriodendron* leaf, or a



Certain forms of leaves of *Liriodendron Tuttipifera*.

leaflet of some species of Leguminosae, preferably the former.

Liriophyllum populoides, the type of the genus, as the winged margins of the petiole show, had advanced several stages in the development of stipules. It is undoubtedly related to the ovate simple forms of the ancestral leaf through a form similar to *Liriodendron alatum*, as was just pointed out, possessing, as it does, the winged petioles of the latter. Lesquereux's two figures of *Liriophyllum populoides* have the petioles broken off, but both show the petiole widening as it descends. In the figure of a young leaf, the wings are in juxtaposition with the leaf blade, while in the older leaf there is an interval of petiole, apparently showing that the wings grew down the petiole as it lengthened. The immature leaf furnishes additional proof of its origin from

a form without the widely spreading base, showing ascending margins, and with but an indication of the spreading basilar extensions or lobes which characterize the mature leaves.

Liriophyllum Beckwithii is either an abnormal form of *L. populoides*, or a further extension and more pronounced development of its salient characters. Of rare occurrence and large size, it may simply represent a leaf of *L. populoides* of extraordinary size and more extensive lobation, induced by favorable conditions of growth, just as we find extraordinarily developed leaves of large size and extensive lobation on especially vigorous shoots from saplings of *L. Tulipifera*.

Sterile soil, lack of humidity, or some similar hard condition may account for the development of the *Liriophyllum* type of leaf. The following facts would seem to imply this: In *L. Tulipifera*, the leaves on the same twigs as the flowers tend to an abbreviated blade. Again, by cutting off the shoots of the year, and forcing next year's buds to take their places, we obtain leaves similar to the above. All of these forms approximate *Liriophyllum*, and hint at its probable mode of origin. That the peculiar ascending primaries offer no objection to this theory is well shown in several small specimens of *L. Tulipifera* leaves in my collection, with a cleft apex and opposite ascending veins. It would require only the slowly increasing development of an opposite-veined and cleft-tip form like this to become the opposite-veined, deeply cleft *Liriophyllum*.

As the Dakota time progressed, *Liriodendron*, fostered by the humid and warm Cretaceous climate, developed rapidly, the leaves increasing greatly in size, and with this went increased lobation, the tendency being for those portions of the leaf blade at the terminals of the secondary veins to increase at the expense of the rest of the blade. These lobes are obtuse where a full or an extra supply of nourishment is obtained, and acute where there is any diminution of the supply. That the congenial warmth, humidity, and rich soil of this period were the primary factors in the great variation and development of the *Liriodendrons* is undoubtedly the case; for in modern tulip trees those

growing in rich soil, or leaves on especially vigorous shoots from old stumps, saplings, etc., show the greatest tendency to variation and large size, and trees in poor soil have smaller acutely lobed leaves, and the leaves on large, mature trees are smaller than those on saplings, and have the lobation reduced almost to cuspidate points. Again, on individual shoots where the supply of nourishment is reduced artificially, or where it is diverted for the formation of flower and fruit, the leaves undergo great reduction in size and lobation, showing a tendency to assume a two-lobed, *Liriophyllum*-like form. There is nothing particularly new in this view, for we find in Lindley's *Introduction to Botany* (p. 136, 1839) the following: "Lobation [of leaves] is deepest and more pronounced in those individuals of the same species whose vegetation has been least favored by humidity, and the nature of the soil."

Large leaves, affording a larger assimilating area, are of course more advantageous in the performance of the functions of vegetation than smaller ones, and some of the additional advantages accruing when these large leaves are lobed instead of simple may be enumerated as follows: The simple leaves are more unwieldy and heavier, and therefore much more easily affected and broken by winds and rain. In the lobed forms the sunlight is more completely utilized; there is economy of circulation through more direct connection of parts; there are more leaves to a given amount of material, and therefore more active assimilating organs. The functional activity of two-lobed leaves, having an area equal to that of a single simple leaf, ought to be considerably greater.

The next stage in the genealogy of *Liriodendron* which has been preserved is *L. giganteum* Lesq., which is reached by a series of slight changes from the more primitive *L. Meekii* through constantly enlarging and more lobate forms induced by the environment indicated above. The petiole has become greatly lengthened, and stipules had probably been developed; for, although we have no trace of stipules except in the winged petioles of *Liriophyllum populoides* of the Dakota and *Liriodendron*

alatum of the Laramie, unless certain forms referred to *Paliurus*¹⁷ are the remains of stipules, they must have been developed early in the history of the group, before the vernation became fixed and the petioles lengthened. *L. giganteum* had a very large leaf, 5 by 16.5 cm, with consequently large veins, oblique or rectangular, oblong, obtuse lobes, and deeply emarginate apex. We have a number of leaf forms of *L. Tulipifera* from particularly luxuriant saplings that greatly resemble *L. giganteum*. The venation is similar; the general contour is similar, the lobes in *L. Tulipifera* being a trifle less obtuse; and, like *L. giganteum*, these are very large leaves, in fact in all extra large leaves of *L. Tulipifera* the tendency is to assume a form that approximates *L. giganteum* in a general way, and we have a number of such forms in our collection. *L. giganteum cruciforme* Lesq. differs but slightly from *L. giganteum*, the lobes being more nearly at right angles and the intervening sinuses deeper and narrower; the lobes are also somewhat less obtuse and more like some of our specimens of *L. Tulipifera*. Dawson's *L. praetulipiferum* from the Upper Cretaceous is evidently related to *L. giganteum*. It also resembles some of the forms of *L. Meekii*, and is without doubt closely related to the then existing ancestor of our modern tulip tree.

The next species in the geological record is *L. oblongifolium* Newb. from the Amboy clays of New Jersey. Among the various published figures of this species all are fragmentary and of more or less uncertain affinity except one figure which shows a leaf surprisingly like the normal mature leaves of *L. Tulipifera*. In fact there can be but little doubt that *L. oblongifolium* is in the direct line of descent leading to *L. Tulipifera*, from which the latter has changed but slightly. *L. oblongifolium* is somewhat less lobate than the modern leaf, and has the lateral veins nearly straight, ascending, and approximately parallel. There is no doubt that *L. oblongifolium*, *L. praetulipiferum*, and *L. giganteum*

¹⁷ See Flora of Amboy clays, *pl.* 23. *figs.* 8, 9; Flora of the Dakota group, *pl.* 35. *figs.* 6, 7; Bull. Torr. Bot. Club 21: *pl.* 177. *fig.* 5; Trans. N. Y. Acad. Sci. 12: *pl.* 2. *figs.* 12, 18, 19.

were very closely related, and probably had a common ancestor. Among the leaves of *L. Tulipifera* we can find a perfect series from *L. oblongifolium* to *L. giganteum* and *L. praetulipiferum* on the one hand, to *L. quercifolium* on the other. The latter was derived from *L. oblongifolium* through leaves with increased lobation.

The next fossil species is *L. pinnatifidum* Lesq., and we note that Lesquereux's two figures of this species differ considerably from each other in shape. Both are fragments, and their nervation is dissimilar and remote from that which obtains in all the other known forms of *Liriodendron*. While one may be a *Liriodendron*, we are forced to consider the other as an altogether different species, possibly allied to *Quercus*, at any rate not related to *Liriodendron*. We note in passing that Lesquereux's *Cissites obtusilobus*, also from the Dakota group (Fl. Dak. 161. pl. 33. fig. 5), somewhat resembles the species under discussion. Lesquereux¹⁸ wrote later of *Cissites* as follows: "Velenovsky, in his *Flora Bohm. Kreideformation*, pt. 2, pl. 6. fig. 2, has a figure like this, and has named it *Liriodendron Cela-kovskii*. It essentially differs in the lateral primaries being basilar." We are inclined to think that this observation is a hint at the true affinity of the specimen, for it has the indefinable look of a *Liriodendron* leaf, and we have in our collection of *L. Tulipifera* leaves several that approximate *Cissites obtusilobus*. *Cissites alatus* Lesq. (Fl. Dak. group, 160. pl. 23. fig. 6. 1891) in all probability also belongs here. Lesquereux was inclined to refer it to *Liriodendron*, and afterward compared it with *L. Gardneri* Saporta, which it greatly resembles. We have also *L. Tulipifera* leaves that resemble it, but somewhat remotely.

The American Cretaceous species of *Liriodendron* at this time diverge somewhat widely from the line of descent leading to the modern form, and develop into some curious lobate forms that will be considered later.

We are obliged to go to Europe to find the stages subsequent to *L. oblongifolium* leading to *L. Tulipifera*. We find them nearly

¹⁸ *Flora Dakota* group, p. 161, footnote.

complete in the forms variously referred to *L. Procaccinii* Unger, *L. Haueri* Ettings., *L. helveticum* Fish-Oester, *L. islandicum* Sap. & Marion, all from the European Tertiary¹⁹ formations, the forms from the Pliocene being clearly identical with the existing species. Schmalhausen²² refers a leaf from the Pliocene (?) of the Altai mountains to *L. Tulipifera*, and Saporta and Marion consider certain of the forms referred to *L. islandicum* as identical with the modern tree.

With the advent of the Glacial period the European Liriodendrons, along with Sassafras, Magnolia, Celastrus, etc., disappeared from that continent, the glacial conditions undoubtedly forcing them southward until further retreat was cut off by the Mediterranean.

Returning to the curious lobate forms from the American Cretaceous, we have four species and one variety that are unlike anything seen in the modern species, and evidently not forming a part of its ancestral line, but a collateral branch from it. The most lobate forms found on the modern tree are quite different from the long, narrow-lobed forms under consideration. The least divergent form is *L. intermedium* Lesq., and it is only known from fragments of the upper part of the leaf. It was evidently a large leaf, and might be derived from a form like *L. giganteum* by an extreme narrowing of the lobes. The next species, *L. Wellingtonii* Lesq., differs from the preceding in having the supposed basal lobes of *L. intermedium* lengthened and curved inward, ascending almost vertically nearly to the tips of the upper lobes. *L. acuminatum* Lesq. differs from *L. Wellingtonii* in having the basal lobes somewhat reduced in length and all of the lobes acuminate. The variety *bilobatum* merely differs from *L. acuminatum* in having the basal lobes bilobate, thus greatly resembling various forms referred to *Aralia*. Lesquereux compares it with *L. islandicum* S. & M. If it be a true Liriodendron

¹⁹ Diligent search fails to disclose Liriodendron in the extensive European Cretaceous system.

²² Ueber tertiäre Pflanzen aus dem Thale des Flusses Buchtornia am fusse des Altaigebirges. Palaeontographica 33. 1887. *L. Celakovskii* Velen. is probably not a Liriodendron (Bull. Torr. Bot. Club, July 1902).

it is certainly a very anomalous form of leaf, and represents the extreme of development of the lobate leaf in this genus.

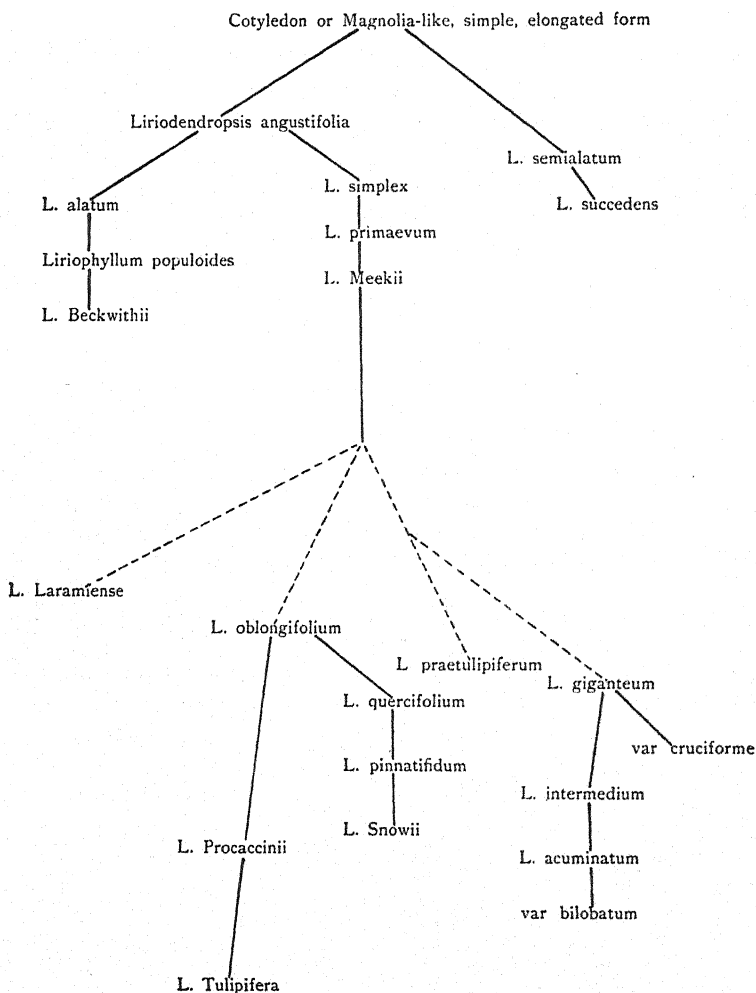
We have next to consider Ward's *L. Laramiense*. It is a more recent species than any of the preceding American forms, being from the Laramie. According to Stanton & Knowlton,²¹ these strata underlie marine Cretaceous and therefore belong to the Montana formation. If this reference be correct, it leaves but one American species besides the existing one subsequent to the Cretaceous. If *L. Laramiense* is a true species, the doubt being caused by the known remains consisting of but the basal fragment of a leaf, it was a comparatively simple form which developed from the ancestral *Tulipifera*-like form, which was probably contemporaneous with it, although as yet no *L. Tulipifera* remains have been found in these strata. Modern simple *L. Tulipifera* leaves similar to *L. Laramiense* are very common.

The last fossil form to consider is the remarkable *L. Snowii* Lesq., from the Dakota group. It is a large leaf, ovate in outline, pinnately divided into several linear, obtuse lobes on each side, which are attached by their whole bases to the midrib, but are entirely separated from each other by a considerable interval of free midrib. While it differs so widely from any of the other forms of *Liriodendron* as to seem to represent an unallied compound leaf, there is something about it that stamps it as a species of *Liriodendron*. The venation is also typical of the genus. It may represent a further and extreme development from *L. pinnatifidum*, which originated, flourished, and disappeared during the deposition of the Dakota group; we certainly have nothing like it among modern *Liriodendron* leaves.

With the close of the Dakota period the *Liriodendron* group seems to wane, having but one or possibly two species in the Laramie, and none in the American Tertiary or more recent formations, although the tulip tree flourished in Europe throughout the Tertiary. While the extremely lobate species may have

²¹ Bull. Geol. Soc. Am. 8: 127-156. 1896.

become extinct after the close of the Cretaceous, it is very probable that the ancestors of the modern tree still flourished, and we can only blame the imperfect geological record for the lack



of evidence of their existence. It would seem that the numerous Tertiary lakes would have furnished abundant facilities for fossilizing leaves from the trees that skirted their shores, or were brought down from the adjacent uplands by the many streams.

Matthew and Davis²² have recently advanced reasons for considering a considerable number of the so-called Tertiary lake formations to be flood-plain and aeolian deposits. If their arguments are sustained, which seems unlikely except for restricted areas, the absence of leaves from these formations becomes explicable. Be this as it may, the record has thus far proved barren, and we can only congratulate ourselves that the more ancient record is so complete. We can better spare the record of the Tertiary, for the modern form became practically fixed in *L. oblongifolium* of the Amboy clays, or its undiscovered, closely related contemporary, and has changed but slightly in subsequent times.

A summary of these suggested relationships may be presented as on opposite page.

PASSAIC, N. J.

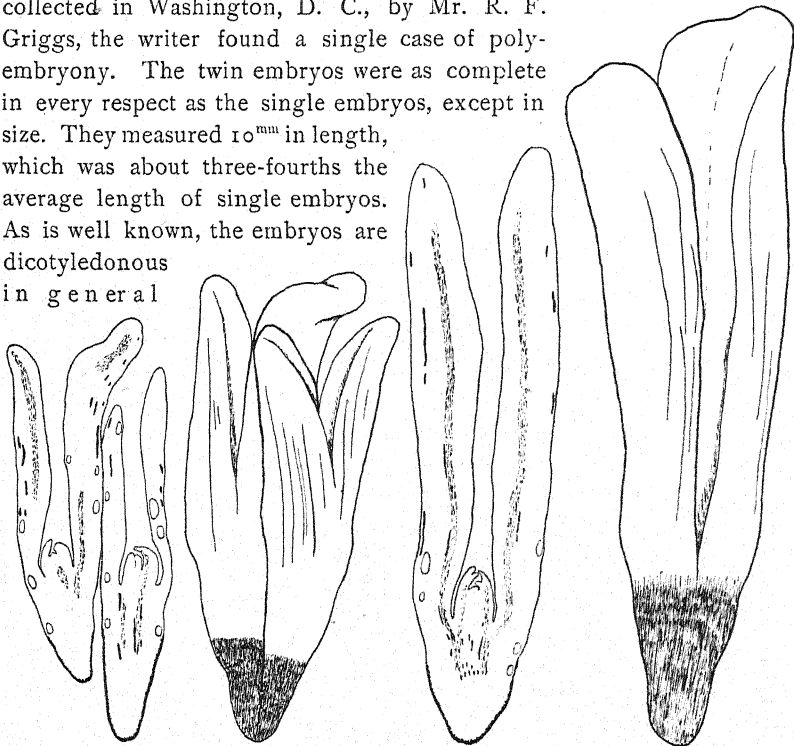
²² MATTHEW, W. D. Bull. Am. Mus. Nat. Hist. 12: 25. 1899; GILBERT, G. K. 17th Ann. Rep. U. S. Geol. Surv. 1895-6, part 2, p. 575; WILLISTON, Kan. Univ. Geol. Surv. Rep. 1896; see also FRAAS in Science 14: 210.

BRIEFER ARTICLES.

POLYEMBRYONY IN GINKGO.

(WITH FOUR FIGURES)

Polyembryony is common among the pines, but I have not seen it recorded for Ginkgo. Recently in examining some material of Ginkgo, collected in Washington, D. C., by Mr. R. F. Griggs, the writer found a single case of polyembryony. The twin embryos were as complete in every respect as the single embryos, except in size. They measured 10^{mm} in length, which was about three-fourths the average length of single embryos. As well known, the embryos are dicotyledonous in general



character, and when sectioned the cotyledons showed an elongation of cells through the long axis, apparently the fibrovascular bundle. The plumules were made up of several leaflets, a branch of the fibrovascular bundle running into each; and near the surface sec-

tions of a number of large resin ducts were observed. The accompanying illustrations are self-explanatory.—MEL T. COOK, *Ohio State University, Columbus, Ohio.*

A ROOT ROT OF APPLE TREES CAUSED BY THELEPHORA GALACTINA FR.

FOR thirty years or more apple growers in West Virginia, Kentucky, southern Illinois, Missouri, Arkansas, and Oklahoma, have lost numerous trees from root diseases of various kinds. The trees attacked were generally young trees, from three to six years old. During the last few years investigations have been carried on in several states, which show that the death of apple and other fruit trees, because of root disease, is due to a number of different diseases; in other words, that the term "root-rot" cannot always be applied to one disease. Several fungi have been associated with root rot diseases. One of these is widely distributed as a parasite of trees in the states mentioned above. Apple trees set out on newly cleared ground are attacked by the fungus very soon after planting. The trees show no signs of disease until the year of death. Diseased trees four and five years old, with their root system almost entirely destroyed, can often be recognized by excessive flower and fruit production, a phenomenon frequently noted when plants are much weakened by disease. Diseased trees die very suddenly, generally in the early summer. The leaves wither and fall and within a few weeks the tree is dead. Diseased trees always occur in groups, which indicates that the fungus spreads through the soil.

The root rot disease caused by *Thelephora* differs from that caused by *Agaricus melleus* in that no signs of disease are evident above ground until the trees are dead. The fungus causing this disease has been identified by Dr. E. A. Burt as *Thelephora galactina* Fr. The fruiting body consists of bright red orange leathery sheets which form on diseased roots and around the base of the trunk. The fungus was transferred from oak roots to young apple trees, killing the latter within a year.

An extended account of the mode of occurrence and growth of *Thelephora galactina* will be published before long.—HERMANN VON SCHRENK, *Shaw School of Botany, St. Louis.*

STIPA HASSEI NOT A GOOD SPECIES.

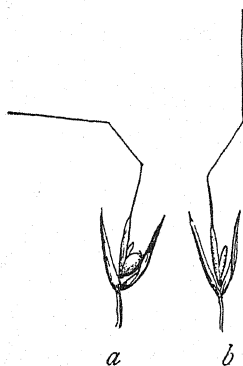
(WITH ONE FIGURE)

IN Contributions from the National Herbarium 1:267. 1893, Dr. Vasey describes several new species of grasses. One of these belongs to the genus *Stipa* and is named *Stipa Hassei* in honor of its collector.

There are five specimens of this species in the National Herbarium, all collected by Dr. Hasse in the region of the Santa Monica range of Los Angeles county, California. The type and a cotype were collected in the spring of 1891, and the other specimens were collected April 5, 1895.

All these specimens are but abnormal forms of *Stipa eminens Andersoni* Vasey, caused by the growth of a smut. The oblong grain, thin glumes, and narrow, short-branched panicles, on which the specific characters of *Stipa Hassei* Vasey are based, are due to the development of this fungus.

In the accompanying figure, *a* shows a spikelet from the type specimen of *Stipa Hassei* Vasey, and *b* a spikelet from the type specimen of *Stipa eminens Andersoni* Vasey. Both are enlarged twice. — ERNEST NORTON WILCOX, Office of the Agrostologist, Washington, D. C.



CURRENT LITERATURE.

BOOK REVIEWS.

A university text.¹

THAT there is need of a good general text-book of botany of university rank, written from the modern standpoint and largely from American material, has long been recognized. Professor Campbell is the first in this field, and his purpose is "to present in as compact a form as possible an outline of the essentials of modern botany." His book treats of anatomy, morphology, general taxonomy, physiology, and ecology, although the chapters are not grouped under such general divisions.

It is a serious question whether the science of botany has not advanced too far for any one man to undertake a general text of university rank. In the nature of things, the writer's own field will be developed much more extensively than the others, which perhaps are equally important as representing the present status of botany. The result will be a university text in one phase of the subject, and a very incomplete and elementary text in the other phases.

It is upon this basis that the book before us must be judged. The matter dealing with general anatomy, morphology, and the outlines of classification, occupies 460 pages. In this field Professor Campbell's standing is assured, and his grasp of the subject and his conclusions are derived from an immense amount of personal investigation. This strong personal element is attractive and useful, even though there may be much diversity of opinion as to many of the statements and conclusions. It is a matter of regret, however, that in a university text so little attention is given to the discussion of such important topics as the origin and evolution of sex, the appearance of the sporophyte, etc. The materials are presented in somewhat encyclopedic fashion, and as the author only intended the book as one of reference, perhaps he has left it to the university teacher to develop his own theories and lines of continuity.

The presentation of physiology occupies only 33 pages, which cannot be claimed to be an adequate expression of the important place of physiology in modern botany, especially from the university standpoint. The great brevity precludes completeness and often clearness, and sometimes

¹ CAMPBELL, DOUGLAS HOUGHTON, A university text-book of botany. 8vo. xv + 579, with 493 figures and 15 plates. New York: The Macmillan Company. 1902. \$4.00.

will probably result in misconception. For example, on p. 464, the independence of water and solutes in entering the cell is ignored, although it is fundamental; and on p. 489 there is hopeless confusion between rheotropism and hydrotropism, fundamentally different phenomena.

In the two chapters devoted to ecology, the style is easy and pleasing, but the presentation is altogether too brief and the matter too simple to satisfy elementary instruction in a university. Many would also object to the extreme teleological standpoint. The whole subject of ecology has been making such rapid development that it has become dangerous for one unfamiliar with the great mass of recent work and literature to venture many statements.

Perhaps the most noticeable feature from the standpoint of an organized text is the lack of any typographical organization of captions. Of course it is troublesome to coordinate captions so as to express the proper relationships of subjects, but it is extremely desirable in a text for elementary instruction, even in universities.

After all, the book will stand for a mass of morphological facts, most of which have passed under the author's observation, illustrated to quite an unusual extent by the author's own drawings, and largely derived in a most desirable way from American material. From this standpoint it is very welcome, and will doubtless be largely used, as its author intended, for a book of reference.—J. M. C.

Saccardo's *Sylloge Fungorum*.

ANOTHER volume of this monumental work, projected and edited by Professor P. A. Saccardo, has come to hand. It is the sixteenth volume,² and is of the same notable size and quality as those preceding. The fifteenth volume, devoted to synonymy, and prepared in collaboration with Professor E. Mussat of Paris, has not yet been distributed, although it was expected to appear in 1901. In the present volume are mentioned 4853 species, representing mycological activity during the preceding eighteen months, *i. e.*, from June 1899 to December 1901. Complete diagnoses are given of all the species except 490, which came in so late that only a citation could be entered at the back of the volume. There is an excellent species and host index, and a universal index of genera. The total number of species of the fifteen volumes now aggregates 52,157. In this volume twenty-seven species are described for the first time, and new names are proposed for five species previously published.—J. C. ARTHUR.

² SACCARDO, P. A., *Sylloge fungorum omnium hucusque cognitorum; supplementum universale, pars V.* Auctoribus P. A. Saccardo et P. Sydow. Adjectus est index totius operis. 8vo, pp. 1291. Patavii, 1902. 81 francs.

MINOR NOTICES.

MISS CLARA E. CUMMINGS has published a list of Labrador lichens collected by Professor E. B. Delabarre on the Atlantic coast of Labrador during 1900. The list is a reprint from Bull. Geog. Soc. Phil. 3 : no. 4, and contains 43 species.—J. M. C.

THE EXPERIMENT FARM of the Horticultural Society of North Carolina has published an attractive pamphlet calling attention to the many valuable qualities of the "cow pea" (*Vigna sinensis*). It is a full synopsis of the history, habits, and merits of the plant.—J. M. C.

IT IS VERY FITTING that Dr. Robert Hartig³ just before his death should have brought together a summary of his publications. The first 52 pages of the work is taken up in brief reviews of his 38 papers. In the remaining portion of the volume the author gives the results of his last work on the influence of gravity, pressure, and pull on the form of the fir and the structure of its wood.—H. N. WHITFORD.

V. KOMAROV has just published⁴ the first volume of a *Flora of Manchuria*, including the vascular plants. All of the notes and descriptive text are in Russian, and the Engler sequence is followed, the volume completing the monocotyledons. The pteridophytes are represented by 74 species, the single new one being a *Nephrodium*; the gymnosperms comprise 29 species, *Pinus funebris* and *Abies gracilis* being new; while the list of monocotyledons numbers 461, new species being described in *Scirpus*, *Carex* (2), and *Lilium*. Of the monocotyledons, 86 are grasses and 122 sedges, *Carex* containing 83 species.—J. M. C.

WULFF⁵ has made some recent contributions to the knowledge of arctic plant ecology. The first paper treats of the transpiration of arctic plants. By means of the cobalt paper method the relative transpiration activity of some ten species, each under sixteen different climatic conditions, were determined. The main conclusions are as follows: daily variation in transpiration is absent; as compared with temperate plants the transpiration is uniformly weak; there is a frequent falling off of transpiration in relatively high temperatures and low humidity. A second paper treats of the occurrence of anthocyan in arctic plants. The distribution of coloring matter is carefully noted in fifty species. Dried specimens were examined and found to contain abundant sugar and little starch. This is in accord with the experiments of Miyake and others, who found cold conducive to the production of

³HARTIG, ROBERT, Holzuntersuchungen. Altes und Neues. vi + 99, with 52 text figures. Berlin : Springer, 1901.

⁴Acta Horti Petropolitani 20 : 1-559. 1901.

⁵WULFF, THORILD, Botanische Beobachtungen aus Spitzbergen. pp. iii + 115, with 4 plates. E. Malmström. 1902.

sugar rather than starch. The author concludes that the excess of sugar causes the appearance of the anthocyan. This conclusion is based upon Overton's experiments. A third paper deals with the distribution of plants on a peculiar formation known as the "Polygonboden." In the last paper the author has collected some miscellaneous floristic notes.—H. N. WHITFORD.

NOTES FOR STUDENTS.

R. KNUTH⁶ has begun the publication of the results of his study of *Geranium*. After the general distribution of the genus is presented, each of the twelve sections is considered separately, the present paper including *Unguiculata* (5 spp.), *Subacaulia* (4 spp.), *Tuberosa* (4 spp.), and *Batrachia* (38 spp.).—J. M. C.

IN A PRELIMINARY PAPER⁷ on chromosome reduction in *Larix leptolepis* Ishikawa announces a condition similar to that described in his paper on *Allium fistulosum*. In the prophase of the first division of the pollen mother cell twelve pairs of chromosomes appear. The chromosomes of the pair may be variously united, sometimes forming tetrads. In the second division twelve ring-shaped chromosomes are formed. The writer interprets the first division as an "equation division," and the second as a "reduction division" in Weissman's sense. The full paper will appear in *Jour. Coll. Sci. Tokyo*.—W. J. G. LAND.

J. M. GREENMAN⁸ has published the general results of his long study of the North and Central American species of *Senecio*. After an historical account of the genus, the morphology of the different plant members is considered, and the classification presented. About 300 species are included, grouped into 22 sections, 14 of which bear Mr. Greenman's name. The subgenus *Eusenecio* O. Hoffm. includes 21 of the sections, and *Pseudogynoxis* Greenm. the remaining one. The species are merely listed under their tribes, 70 of them being unpublished new species. The geographical distribution of the genus as a whole and of each section is presented in concise and tabulated form.—J. M. C.

A NEW INTERPRETATION of the phenomena of sap pressure and bleeding has been set forth by Molisch.⁹ He takes the position that all the cases

⁶Über die geographische Verbreitung und die Anpassungserscheinungen der Gattung *Geranium* im Verhältnis zu ihrer systematischen Gliederung. Engler's Bot. Jahrb. 32: 190-208. 1902.

⁷ISHIKAWA, C., Ueber die Chromosomenreduction bei *Larix leptolepis*. Beih. Bot. Centralb. 11: 6-7. 1901.

⁸Monographie der nord- und centralamerikanischen Arten der Gattung *Senecio*. Engler's Bot. Jahrb. 32: 1-33. 1902.

⁹MOLISCH, HANS, Ueber lokalen Blutungsdruck und seine Ursachen. Bot. Zeit. 60: 45-63. 1902.

of bleeding which have been observed are pathological phenomena, dependent either upon the stimulus of the wound by which the manometer was brought into the tissue, or upon the development of abnormal tissue (such as callus) covering the wound surface. The pressure arises, then, at or near the wound surface and not far back in the plant body. Many experiments were performed upon *Juglans regia*, *Betula alba*, etc., and all seem to support this idea. The work of Figdor, C. Kraus, Pitra, and Wieler is discussed, and evidence drawn therefrom in support of the new interpretation.—B. E. LIVINGSTON.

M. T. COOK¹⁰ has published the results of a morphological study of *Castalia* (*Nymphaea*) *odorata* and *Nymphaea* (*Nuphar*) *advena*. The development of the megaspore and of the structures of the embryo sac is reported as presenting no new features. The first division of the definitive nucleus is followed by a wall across the embryo sac. In the upper chamber the endosperm develops, while the lower extends as an haustorial tube to the chalazal extremity of the ovule. The embryo is at first a spherical multicellular mass, as described by Lyon and Conard, and later forms what the author, in agreement with Lyon, regards as a single cotyledon. Following Lyon, he would regard this as justifying the transfer of the Nymphaeaceae to the monocotyledons.—J. M. C.

MISS SIBILLE O. FORD¹¹ has been studying the anatomy and development of *Ceratopteris thalictroides*. She finds that the plant is annual, and is often reproduced by adventitious buds originating in the angles between the lobes of the leaves. The bundles are generally bicollateral, and the cauline bundle system consists of an outer series of large strands and of smaller medullary strands. The developing stelar system does not pass through a siphonostelic phase as in most ferns with numerous vascular strands; but, like certain Nymphaeaceae, breaks up immediately and becomes polystelic. The sporangia are large, and have an imperfectly developed annulus. Miss Ford considers *Ceratopteris* to be closely allied to the Polypodiaceae, and also to show less marked affinities with the Marsiliaceae.—E. C. JEFFREY.

ROSENVINGE¹² contributes a paper on spiral position of leaves in several species of Polysiphonia. It is somewhat polemic, being directed against Seckt. His figures are meager for the immense amount of mechanics involved. He refutes Schwendener's contact theory, and makes clear the fact that the position of the leaf depends upon the position of the daughter

¹⁰ Development of the embryo sac and embryo of *Castalia odorata* and *Nymphaea advena*. Bull. Torr. Bot. Club 29: 211-220. pls. 12-13. 1902.

¹¹ The anatomy of *Ceratopteris thalictroides* (L.), Annals of Botany 16: 95-121. pl. 6. 1902.

¹² ROSENVINGE, L. KOLDERUP, Ueber die Spiralstellungen der Rhodomeleaceen. Jahrb. Wiss. Bot. 37: 338-364. pl. 6. 1902.

nucleus and the direction of the segment wall. The nucleus assumes such a position long before the wall appears. The leaf immediately below is rarely of sufficient length to reach the apical cell, as Schwendener assumes, and even when it does, stands out from the axis at a very appreciable angle. Even though there appears to be a correlation between the position of the lower leaf and the direction of the segment wall, we must look for some more hidden stimulus than mere physical contact.—JAMES J. WOLFE.

A. G. TANSLEY and MISS R. B. LULHAM¹³ in a preliminary note describe a new type of fern stele in species of *Lindsaya* from the Malay peninsula and elsewhere. The tubular central cylinder has permanently a core of phloem only, and is of considerable interest because it presents in the adult a condition which is a developmental phase only in other siphonostelic ferns. In the same number of the *Annals* GWYNNE-VAUGHN¹⁴ describes a curious axillary organ in *Helminthostachys zeylanica*. He suggests that the structure in question may be a vestigial axillary bud, or perhaps of glandular nature. T. G. HILL¹⁵ makes a preliminary announcement of the discovery of a cambium in the fibrovascular strands of *Angiopteris evecta*. L. A. BOODLE¹⁶ also describes lignification of the phloem in *Helianthus annuus*. Treatment of the sieve-tubes of old stems with phloroglucin and hydrochloric acid brings about the pink lignin reaction, not only in the walls but also in the contents of the tubes.—E. C. JEFFREY.

HUS¹⁷ has published a systematic account of the species of *Porphyra* of our Pacific coast, with notes on structure and distribution. One is surprised to learn the great length of some of these plants, 325 cm being recorded for a specimen of *P. perforata lanceolata*, and over three meters for *P. nereocystis*. There are two forms of attachment; the usual one discoid, and made up of rhizoidal filaments; and the second a cushion-like parenchymatous type. The latter is peculiar to *P. naiadum*, which occurs on *Phyllospadix* and *Zostera*, and results in certain interesting peculiarities of growth and structure. The cushion is at first a single layer of cells in thickness, and by marginal growth extends over the leaf surfaces of the eel grass. An indefinite number of fronds may develop from this cushion, any superficial cell having the power of growth. The cushion is therefore a preliminary phase

¹³ On a new type of fern stele, and its probable phylogenetic relations. *Annals of Botany* 16: 157-164. 1902.

¹⁴ On an unexplained point in the anatomy of *Helminthostachys zeylanica*. *Idem*. 170-173.

¹⁵ On secondary thickening in *Angiopteris evecta*. *Idem*. 173-174.

¹⁶ On lignification in the phloem of *Helianthus annuus*. *Idem*. 180-183.

¹⁷ Hus, T., An account of the species of *Porphyra* found on the Pacific coast of North America. *Proc. Cal. Acad. Sci. Bot.* 2: 173-238. pls. 20-22. 1902.

of the *Porphyra* plant, analogous to the *Chantransia* condition of *Batrachospermum*. It is a very advantageous adaptation to insure the continuous production of numerous fronds. No new facts are presented respecting the problem of sexuality in this group, but the observations are rather against the statements of Berthold.—B. M. DAVIS.

IN A SECOND PAPER on the influence of tensions upon cell growth and the direction of new walls Kny¹⁸ concludes that when no other factors are effective, growth takes place in the direction of a pull and at right angles to that of a compressing force. Cross walls seek a direction perpendicular to external pressure upon the dividing cell, but parallel to a stretching tension exerted upon it. There are "internal forces" at work in most living tissues, which tend to prevent this reaction to tensions, "heredity" being apparently the main one. This means, if we judge correctly, that the above principle does not nearly always hold true, but that the direction of growth and of wall-formation is mainly controlled by as yet unknown factors. Perhaps the most definite result of experimentation here recorded is one obtained, at the suggestion of the author, by M. Nordhausen on segmenting eggs of *Fucus*. Although the first walls in these eggs are normally formed at right angles to incident light, when the eggs are compressed between glass plates these walls always appear perpendicular to the plates, no matter if this direction be parallel to the incident light rays. Kny experimented upon roots of *Vicia*, *Malva*, *Raphanus*, tubers of *Ullucus*, and stems of *Impatiens*, *Begonia*, *Bryophyllum*, *Ampelopsis*, *Salix*, etc. Two plates showing the effect of tensions upon the different tissues accompany the paper.—B. E. LIVINGSTON.

DR. D. H. SCOTT¹⁹ has recently published an account of some interesting fossil stems, chiefly from the Lower Carboniferous of Scotland. Although the specimens described have the *Dadoxylon* or *Araucarioxylon* type of secondary wood, they differ strikingly from other known stems of *Cordaite*s in the possession of mesarch bundles of primary xylem. The fossils are grouped under three genera, *Calamopitys*, *Pitys*, and *Dadoxylon*. *Calamopitys* is characterized by a small pith, surrounded by a few comparatively large mesarch primary wood bundles, and a thick zone of secondary wood. *Pitys* possesses a very large medulla and numerous mesarch primary strands, which are separated from the secondary wood by a broad interval of parenchyma. Of the third type of stem, *Dadoxylon Spencersi*, Dr. Scott writes: "The importance of *D. Spencersi* lies in its being on the one hand a typical *Dadoxylon*, with the type of secondary wood which we know belonged to *Cordaite*s, while

¹⁸ KNY, L., Ueber den Einfluss von Zug und Druck auf die Richtung der Scheidewände in sich theilenden Pflanzenzellen (Zweite Mittheilung). Jahrb. Wiss. Bot. 37: 55-98. 1901.

¹⁹ On the primary structure of certain Palaeozoic stems with the *Dadoxylon* type of wood. Trans. Roy. Soc. Edinburgh 40²: 331-365. pls. 1-6. 1902.

on the other hand it shows in a reduced form primary xylem comparable to that of *Lyginodendron* or *Poroxyton*. It suggests, perhaps more strongly than any of the other species described, a truly gymnospermous stem, which may well have belonged to one of the Cordaiteae, but which still retains the last relics of the primary wood-structure characteristic of the Poroxytonae and the *Lyginodendreae*." The article is illustrated by six plates, two of which are photographic.—E. C. JEFFREY.

L. A. BOODLE²⁰, in the third of his studies on the anatomy of ferns, supplements the observations of Poirault on the *Gleicheniaceae* in several important respects. One species, *Gleichenia pectinata*, departs from the protostelic type of central cylinder described by Poirault for a number of other species of the genus in possessing a siphonostelic (solenostelic) cauline fibrovascular system. The stelar tube has internal as well as external phloem and endodermis. Boodle differs from Poirault in his morphological interpretation of the curious masses of brown sclerenchyma surrounded by an endodermis, which are often found embedded in the foliar traces of the *Gleicheniaceae*. Poirault regards them, even where not actually continuous with the similar very characteristic sclerenchyma of the cortex, as cortical sequestrations included by the stelar tissues. On the other hand, Boodle thinks, because the islands of brown sclerenchyma are sometimes continuous with similar cortical tissue and sometimes not, that no argument for their morphological nature can be drawn from continuity with the cortex or its absence. A complete description is given of the anatomy of the rare and interesting north Australian genus *Platyzoma*. The central cylinder is siphonostelic with an internal endodermis but no internal phloem. The foliar gaps in this monotypic and extremely xerophytic genus are much more reduced than is the case in the somewhat similar central cylinder of the *Osmundaceae*.—E. C. JEFFREY.

THE MUCH-NEEDED PROTHALLIUM of *Phylloglossum* has been obtained and studied by A. P. W. Thomas of Auckland, New Zealand. A preliminary account²¹ has been published, but the detailed account, with drawings, is in hand for publication. Although adult plants were abundant, prothallia were very rare, being discovered in only three localities. It is suggested that one of the conditions lacking for the general and annual development of prothallia is the presence of the fungus symbiont that occurs always within the gametophyte. The prothallium is of the subterranean, tuberous type expected. At first an oval tuber is formed, from which arises a cylindrical

²⁰ Comparative anatomy of the *Hymenophyllaceae*, *Schizaeaceae*, and *Gleicheniaceae*. 3. On the anatomy of the *Gleicheniaceae*. *Annals of Botany* 15:703-747. *pls.* 38-39. 1901.

²¹ THOMAS, A. P. W., Preliminary account of the prothallium of *Phylloglossum*. *Proc. Roy. Soc. London* 69: 285-295. 1902.

shaft more or less elongated, dependent probably on the depth of the primary tuber. The top of the cylindrical body becomes expanded in various ways and bears the first sex-organs. Finally the whole structure becomes very irregular, and the whole upper part of the mature prothallium is green, excepting the conspicuous archegonial necks. The antheridia and archegonia seem to differ in no important particular from those of *Lycopodium*. The embryo, immediately on its escape from the prothallium, forms the protocorm, whose "pedicel" elongates and thrusts it to a safe depth (about 3^{mm}). Crie's claim that he sowed the spores of *Phylloglossum* and obtained a colorless prothallium like that of *Ophioglossum* can only be explained on the hypothesis that he saw merely the primary tuberous portion of the prothallium, for the later and conspicuous part becomes even vividly green. On the whole, the prothallium resembles that of *Lycopodium cernuum* nearer than any other. Bower's observations of the occasional branching of the strobilus, and of a leaf some distance below the strobilus, are confirmed; but this leaf was always a sterile sporophyll, and no transition between protophyll and sporophyll was observed. Bertrand's claim that *Phylloglossum* is a reduction form on account of its semiaquatic habit is controverted by the fact that the plants grow better on a hilltop than on the slope, and Thomas never found them in an actual swamp. The writer inclines to the view of those who regard *Phylloglossum* the most primitive of living Lycopodiales.—J. M. C.

KARSTEN, in describing the embryology of the Juglandaceae,²² emphasizes features in which this group resembles the gymnosperms, and expresses his belief that the angiosperms are derived from the gymnosperms, *Gnetum* being the point of contact. The forms studied were *Juglans regia*, *J. cordiformis*, *J. nigra*, *Pterocarya fraxinifolia*, *Carya amara*, and *C. tomentosa*. In *Juglans cordiformis* at the time of fertilization, and even later, the union of the carpels is delayed, thus leaving the ovules exposed, so that the condition hardly differs from that in those gymnosperms with orthotropous ovules, as *Gnetum*. There is an extensive sporogenous tissue in the nucellus, but any further development is usually restricted to a single cell in the median plane. The megaspore mother cell may develop directly into the embryo sac, or may first give rise to a row of three or four megaspores, the two upper of which never develop, but the two lower seem to have an equal chance. Many cases were found in which there were two embryo sacs in the median plane, lying one above the other, sometimes touching each other at the ends, but often separated by several layers of sterile cells. A case is figured in which the sac nearest the chalaza had been fertilized. In *Juglans nigra* the egg cannot be distinguished from the synergids before fertilization. There is probably no fusion of the polar nuclei, and if it takes place at all it occurs

²² KARSTEN, GEO., Ueber die Entwicklung der weiblichen Blüten bei einigen Juglandaceen. *Flora* 90:316-333. *pl.* 12. 1902.

very late. Double fertilization was observed, and the writer believes that in all cases the union of the male nucleus with the polar nucleus takes place earlier than the fertilization of the egg. Although the occasional occurrence of ambisporangiate flowers may indicate a reduced rather than a primitive condition, the Juglandaceae are to be regarded as one of the lowest families of the angiosperms.

Professor Karsten's arguments for the derivation of angiosperms from gymnosperms are based upon embryological characters, and the most important points are well summed up in his diagrammatic comparison of the embryo-sacs of *Gnetum* and the angiosperms, as follows:

<i>Gnetum</i>		<i>Angiosperms.</i>
Prothallium in lower part	=	Antipodals.
Egg cells	=	Egg cell and synergids.
Endosperm nuclei	=	Polar nuclei.
The stimulus to development of embryo and endosperm by fertilization of at least two egg cells.	=	The stimulus to development of the embryo by fertilization of the egg, and development of endosperm by vegetative reproduction.

CHARLES J. CHAMBERLAIN.

ITEMS OF TAXONOMIC INTEREST are as follows: J. K. SMALL (*Torreya* 2: 74. 1902) has described a new *Helianthus* from the sea beach of Florida.—F. S. EARLE (*Bull. N. Y. Bot. Garden* 2: 331-350. 1902) has published the first of a series of papers entitled "Mycological studies." It contains the announcement of the genus *Ascocorticium* in North America; a synopsis of the North American species of *Periconia*, 11 being recognized, 3 of which are new; and descriptions of 28 new fungi, *Hypodermopsis* (*Hypodermataceae*) and *Ohleriella* (*Amphisphaeriaceae*) being new genera.—R. S. WILLIAMS (*idem* 351-380. *pls.* 34-39) has published a preliminary list of Montana mosses, including new species of *Dicranum* and *Barbula*.—R. PILGER (*Engler's Bot. Jahrb.* 32: 53-55. 1902) has described a new African genus (*Acritochaete*) of grasses (*Paniceae*).—W. SCHMIDLE (*idem* 82) has described a new African genus (*Characiella*) of *Protococcaceae*.—A. ENGLER (*idem* 108-125) has described the following new African genera: *Lepidobotrys* and *Nectaropetalum* (*Linaceae*), *Pedaliophyton* (*Pedaliaceae*), and *Pistaciopsis* (*Simarubaceae*).—E. GILG (*idem* 139) has described a new African genus (*Dekindtia*) of *Oleaceae*.—V. S. WHITE (*Bull. Torr. Bot. Club* 29: 251-280. *pls.* 14-18. 1902) has published a revision of the *Nidulariaceae* of North America, *Cyathia* P. Br. (*Cyathus* Haller) containing thirteen species, one of which is new; *Crucibulura* Tul. with one species; *Nidula*, a new genus containing two species, one of them new; and *Granularia* Roth with three species, two of them new.—MARSHALL A. HOWE (*idem* 281-289) in "Notes on American Hepaticae," discusses *Cephalozia connivens*, *Telaranea*, *Arach-*

niopsis, and *Riccia Campbelliana*.—DAVID GRIFFITHS (*idem* 290-301) has described new western species of *Tilletia* (2), *Ustilago*, *Sorosporium* (2), *Gymnoconia*, *Puccinia* (3), *Æcidium* (2), and *Claviceps*.—ELMER D. MERRILL (Bull. 9, Bureau Plant Industry, Depart. Agric.) has published a revision of the North American species of *Spartina*, recognizing nine, one of which (*S. Bakeri* from Florida) is new.—C. R. ORCUTT (West Am. Sci. 12: 163-164. 1902) has described new species of *Mamillaria* (2) and *Echinocactus*.—A. P. MORGAN (Jour. Mycol. 8: 4. 1902) has described a new genus (*Acontium*) of fungi related to *Cephalosporium*, and containing three new species.—B. L. ROBINSON (Rhodora 4: 135-137. 1902) has described a new species of *Hypericum* (*H. Bissellii*) from Connecticut.—M. L. FERNALD (*diem*—) has described a new species of *Scutellaria* (*S. Churchilliana*) from Maine.—H. M. HALL (Univ. Calif. Publ. Bot. 1: 1-140. pls. 1-14. 1902) has described from the San Jacinto mountain new species of *Elymus*, *Stipa*, *Oxytheca*, *Potentilla* (2), and *Erigeron*.—J. M. C.

THE RUSTS OF CEREALS, especially the question of the transmission of the disease by means of the seed, is made the subject of a recent paper by Dr. J. Eriksson²³ in the first two issues of the *Annales des Sciences Naturelles* of the present year. The author reviews the sets of experiments made during the years 1892 to 1899 to grow wheat, oats, and barley in pots protected from atmospheric contagion by glazed cases of different designs, or by inserting the part above ground of single plants into stoppered glass tubes. In spite of the most careful protection rust appeared on the plants. The possible sources of this infection are discussed in detail, and by a process of exclusion the conclusion is reached that it came through the seed, and not from spores floating in the air, as generally assumed. In taking up the problem of the form in which the fungus hibernates in the seed, it is shown that the generally accepted view, that the mycelial life of the yellow rust (*Puccinia glumarum*) may extend throughout the winter and up to the following harvest time, is most likely an error. It is more probable that the rust which persists through the winter dies out in spring, and that both the yellow rust (*P. glumarum*) and the black rust (*P. graminis*) possess mycelium having about the same life period, and that the summer infection for both originates in essentially the same manner. Seeds from rusted plants, it is asserted, are capable of giving rise to rusted plants, with no external source of infection; and the author believes that the rust fungus exists in the seed in a mycoplasmic form, and may so exist as long as the seed is viable. Seeds sometimes bear sori filled with teleutospores, but it is not from these spores that the infection is derived.

While it is impossible to demonstrate the mycoplasm, the fungus for the

²³ Sur l'origine et la propagation de la rouille des céréales. Ann. Sci. Nat. Bot. VIII. 15: 1-160. pls. 1-5. 1902.

time having lost definite form and become intimately associated with the protoplasm of the host, yet many observations and experiments are arrayed by the author in proof of its existence. Moreover, certain analogous states have been observed in other organisms. Among the most striking instances are *Rozella* and *Woronina*, belonging to the Chytridineæ, and parasitic on *Saprolegnia*. According to the studies of Cornu and Fischer, when these plants penetrate the host they become diffused for a time in the protoplasm of the cell, and are then quite unrecognizable. Afterward they assume the usual form and produce spores. In accordance with this theory rust may be checked by treating the seed in a manner to kill the mycoplasm. A change of climate, conditions of growth, etc., may also cause the death of the mycoplasm, which will account for the fact that seed from rust-infested fields when taken to another locality or a distant country often gives plants free from that particular kind of rust.

In the third part of the paper the author discusses the various points raised by different writers who have expressed an opinion upon the subject. Only two American mycologists are mentioned, H. L. Bolley and M. A. Carleton. The paper closes with a bibliography of works cited, naming over forty authors and probably twice as many titles.—J. C. ARTHUR.

NEWS.

PROFESSOR C. S. SARGENT has been elected a foreign member of the Linnean Society of London.

MR. C. G. PRINGLE, the veteran collector, has been appointed keeper of the herbarium of the University of Vermont.

PROFESSOR M. TREUB will be absent from Buitenzorg from May, 1902, to March, 1903, his address being Amsterdam.

SIR WILLIAM THISELTON-DYER, director of the Kew Gardens, has been appointed to the post of "Botanical Adviser" to the colonial Secretary of State.

DR. WILLIAM J. GIES, adjunct professor of physiological chemistry in Columbia University, has been appointed consulting chemist to the New York Botanical Garden.

DR. E. C. JEFFREY, Instructor in botany in the University of Toronto, has accepted a call to Harvard University, bearing the official title Assistant Professor of Vegetable Histology and General Morphology.

PROFESSOR D. H. SCOTT has been elected Botanical Secretary of the Linnean Society to succeed Mr. B. D. Jackson, who has served in that capacity since 1880, and who now becomes General Secretary.

DR. F. L. STEVENS, instructor in charge of the department of biology of the North Carolina College of Agriculture and Mechanic Arts, has been promoted to the full professorship, and also appointed consulting biologist to the Experiment Station.

MISS LAETITIA M. SNOW has been awarded the fellowship given by the Baltimore Association for the advancement of University Education of Women. She will use the fellowship in continuing her botanical studies at the University of Chicago.

A VERY PRETENTIOUS "art portfolio," entitled "La grande flora de Colorado de Montana y Llanos," has been published by Frank S. Thayer, of Denver, Colorado. The only interest to botanists is that the series consists of illustrations, reproduced from water colors, of twelve "native wild flowers." The descriptions were prepared by Mrs. S. B. Walker, the well-known collector and cultivator of Colorado flowers. Her work has been exceptionally well done, excepting in so far as she has been handicapped by the requirements of publication and lack of competent proofreading.

THE *Journal of Mycology* has been revived by its founder, Professor W. A. Kellerman, now of Ohio State University. The original editors, Messrs. Kellerman, Ellis, and Everhart, conducted it for four years, when it passed under the control of the U. S. Department of Agriculture. Under this arrangement three volumes (1889-1894) were issued. After an interval of eight years it has now reappeared as a quarterly, the first number of the eighth volume being published in May last. Such a journal should find ample support among the rapidly increasing number of professional mycologists. The annual subscription is one dollar.

THE SUBJECTS for the Walker prizes in Natural History, of interest to botanists, are as follows: For 1903, "A monograph of any genus or group of Thallophytes;" for 1904, (1) "The reactions of organisms to solutions considered from the standpoint of the chemical theory of dissociation," (2) "Relations of plants to electricity," (3) "A statistical study of the relative cross-fertility between the varieties of a species." For the best memoir a prize of \$60 may be awarded. If, however, the memoir be one of marked merit the amount may be increased to \$100 at the discretion of the committee. Information concerning the details of the competition may be obtained from Glover M. Allen, Secretary, Boston Society of Natural History.

AS A RESULT of a series of experiments begun at Clemson College in 1901, and brought to a successful completion in the laboratories of the New York Botanical Garden, Dr. Alex P. Anderson has developed a method by which, with the application of heat to starch grains and to air-dry starch in many forms, the granules or particles are expanded many times their original dimensions, being fractured into innumerable fragments during the process. As a result of this treatment a grain of rice is expanded to eight or more times its original volume, while still retaining its original form. Other cereals exhibit similar behavior. The process is applicable to nearly all starchy seeds and starchy substances, greatly increasing their nutritive availability. The products obtained are pleasant to the taste, and the process may be varied to produce a great variety of flavors with any given cereal. Furthermore, the material prepared in this manner is absolutely sterilized and may be preserved or stored for long periods. The approval the products have met from food and chemical experts suggests that the process may prove of great economic and commercial value.

BOTANICAL GAZETTE

AUGUST, 1902

THE ELECTRICAL CONDUCTIVITY OF PLANT JUICES.

FRED. D. HEALD.

(WITH TWO FIGURES)

WITH the recent rapid development of physical chemistry, the physiologist has recognized the fact that the application of the methods of physical chemistry to problems of plant physiology is highly important. Already fruitful results have been obtained in a number of lines, and it only remains for future investigations to increase and supplement them. Since "the conductivity of electrolytic solutions stands in direct relationship with certain phenomena," particularly with the osmotic pressure and with the depression of the freezing-point, it has seemed possible that the determination of the electrical conductivity of plant juices, which are themselves electrolytes, might yield interesting results. Some determinations of this character have been carried out, and although the results are not all that might be expected, they are, to say the least, promising, and will be recorded in the following pages.

The conductivity of electrolytes has been an especially prominent subject in the investigations of physical chemistry, so much so that it may almost be called the *Leitmotiv*. The methods of these investigations and the principles established have recently found application outside the province of physical chemistry. A number of instances may be mentioned. The Division of Soils, U. S. Department of Agriculture, has used the electrical conductivity methods for determining the moisture content¹ of

¹ Bulletin no. 6; also no. 12.

arable soils, and also for determining the temperature² and the soluble salt content³ of soils. Oker-Blom⁴ has determined the conductivity of blood, serum, and defibrinated blood for cattle and hogs, but rather from the standpoint of the physical chemist than from that of the physiologist. Recently the rate of flow of underground water⁵ has been determined by conductivity experiments.

APPARATUS.

Since the apparatus used is probably not familiar to the majority of botanists it will be described more in detail than

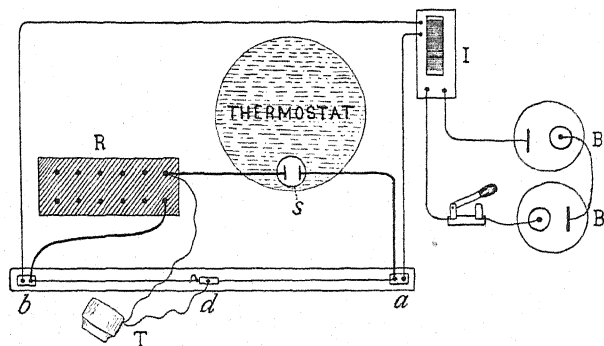


FIG. 1.—For explanation see text.

would otherwise be justifiable. The general plan of the apparatus is represented in *fig. 1*. It consists essentially of a Wheatstone bridge in which the galvanometer is replaced by a telephone (*T*). The resistance is measured along the wire *adb*, which is one meter long, and stretched along a board provided with a millimeter scale. The resistance-box *R* contains resistances of 1, 10, 100, 1000, etc., ohms, and is used for putting into the circuit a resistance nearly equal to that of the electrolytic cell *s*. In order to secure a uniform temperature for all measurements, the electrolytic cell *s* is placed in a thermostat. The windmill thermostat, such as is used in the laboratory of physical chemistry at Leipzig, is the most practical. According to Kohlrausch

² Bulletin no. 7.

⁴ Pflüger's Archives 79: 111-145.

³ Bulletin no. 8.

⁵ Science 14: 972, 1901.

polarization effects can be avoided by using an alternating current of high frequency, and consequently a small induction coil (*I*) of very rapid vibration is added, which serves to transform the current derived from the batteries (*B*).

Since the resistance of solutions varies within wide limits, it was necessary to try a number of different kinds of cells before one was found that was adapted to the work in hand. The first form of cell tried is shown in *fig. 2a*. It has a diameter of 2^{cm}, and the platinum electrodes (*e*) are fused into the ends of glass

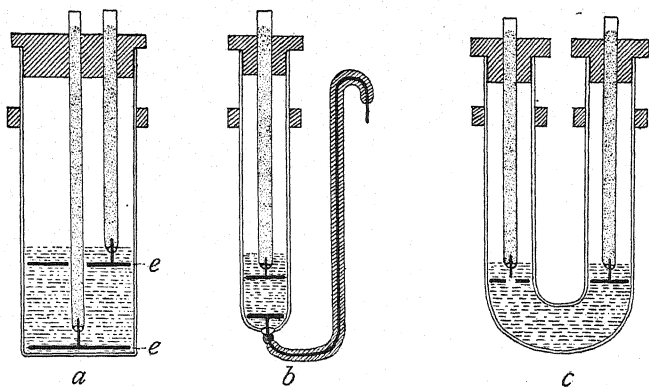


FIG. 2.—For explanation see text.

tubes, which are filled with mercury, and securely set in the hard rubber stopper so as to keep the electrodes in a fixed position. The electrodes are covered with a layer of platinum-black by electrolyzing a dilute solution of platinic chloride between them, the object being to increase the surface of the electrodes and thus minimize the polarization effects. This type of cell was found objectionable for two reasons: first, on account of the amount of juice necessary to cover the electrodes; second, because of the small resistance offered, thus making a very indistinct minimum with the telephone. The second form of cell is shown in *fig. 2b*. The diameter of the cell was 8^{mm}, and consequently the resistance of a small amount of solution could be measured, but the minimum obtained with the telephone was indistinct. The form of cell which proved most satisfactory is

shown in *fig. 2c*. In this U-cell the minimum obtained with the telephone was distinct, the amount of resistance inserted in the resistance-box varying from 500 to 2,000 ohms. The diameter of the tube was 6^{mm}, and 5^{cc} of solution was amply sufficient to cover the electrodes.

In order to extract a small amount of juice from the roots, stems, or leaves of plants a special form of press was necessary. This press and the method of obtaining the extract have been previously described.⁶

METHOD.

The capacity of the electrolytic cell must first be determined. This is done by introducing in the cell a solution of known specific conductivity. For this purpose a $\frac{1}{50}$ normal solution of potassium chloride was used, and the thermostat was kept at a temperature of 25° C. This was the temperature at which all subsequent measurements were made, the uniform temperature being necessary, since the conductivity of electrolytes varies with the temperature. After closing the circuit and starting the coil, the movable contact (*fig. 1, d*) is pushed along the graduated resistance *ab* until the minimum for the telephone is found. The resistances are then in the following ratio :

$$R : bd :: s : ad .$$

For the resistance,

$$s = \frac{R \cdot ad}{bd} ;$$

and for the conductivity,

$$\frac{1}{s} = \frac{bd}{R \cdot ad} .$$

The solution used was one of known specific conductivity *l*, so we have the following relation :

$$l = k \times \frac{bd}{ad \cdot R} \quad \text{or} \quad k = l \times \frac{ad \cdot R}{bd} .$$

$1 = 0.002765$,⁷ and from the readings made the value of *k*, or

⁶ Jour. Appl. Micr. and Lab. Methods 5 : 1679. March 1902.

⁷ LEBLANC, *Electrochimie* (2^{te} Auflage), p. 77, gives the specific conductivity of $\frac{1}{50}$ normal KCl at 25° C. as 0.002765.

the constant for the cell, can be determined. If now the solution of potassium chloride be replaced by the juice which has an unknown conductivity, and the minimum again found for the telephone, we have the new value from which the specific conductivity can be determined:

$$\text{Specific conductivity} = k \times \frac{bd}{R \cdot ad}.$$

MEASUREMENTS.

With the apparatus and according to the method just described measurements were made to determine the conductivity of the juice obtained from different parts of plants. The following list represents those species used: *Beta vulgaris*, *Solanum tuberosum*, *Allium cepa*, *Raphanus sativus*, *Nuphar advena*, *Cucumis sativus*, *Amarantus retroflexus*, *Portulaca oleracea*.

I. BETA VULGARIS.

A number of preliminary measurements were made with the juice extracted from the blades of the leaves, the petioles, and the roots, with the following result as an example:

	Specific cond. of juice			
Blades of leaves	-	-	-	0.03652
Petioles	-	-	-	0.03652
Root	-	-	-	0.01891

It will be noted from these results that the specific conductivity for blades of leaves and petioles is the same, hence in the subsequent measurements leaf-blades and petioles are taken together. In order to determine if there was any relation between the conductivity and the amount of ash present in the juice, the crude ash present in 5 cc of the juice was found. The crude ash was afterwards dissolved in distilled water, diluted up to the original volume of the juice and the specific conductivity of this solution determined. The result is shown by the following:

	Sp. cond. of juice	Crude ash from 5 cc	Sp. cond. of ash sol.
Leaves	0.02676	0.1657 gms	0.0296
Root	0.01349	0.0626	0.01105

The conductivity of the juice from the leaves is shown to be double that obtained from the root, and the amount of crude ash is in accord with this fact, although the juice from the leaves has a little more than twice as much crude ash as is found in the juice from the roots. Since perfectly pure water may be considered as practically a non-conductor, it is evident that the conductivity of the juice obtained is due to the substances that were dissolved in the cell sap. From the results obtained for the specific conductivity of the solution containing the ash, it will be seen that the conductivity is due in large measure to the dissolved salts, and that the organic products have played only a slight part if any.

It may be noted here that these facts are in accord with the general statements in regard to the ash content of plants:⁸ "that the proportion of ash increases from the root upwards to the leaves." The different varieties of *Beta vulgaris* analyzed by Wolff⁹ showed that the leaves contained a much larger amount of crude ash than the roots. It would seem then that the conductivity measurements are here a rough estimate of the relative amounts of ash present in roots and leaves. It must not be forgotten, however, that the juice obtained would not contain all the ash, since some constituents of the ash exist in the plant in the form of insoluble compounds.¹⁰

2. SOLANUM TUBEROSUM.

Young vigorous plants grown on a heavy black loam were used and measurements made for the juice extracted from the leaves, the aerial stems, and the tubers. The results obtained were as follows:

	Sp. cond. of juice	Crude ash from 5 cc	Sp. cond. of ash sol.
Leaves	0.01959	0.0906	0.01857
Aerial stems	0.02449	0.0781	0.02031
Tuber	0.01505	0.0623	0.01516

⁸ VINES, Physiology of plants, p. 130. 1886.

⁹ WOLFF, Aschenanalysen, pp. 76-77.

¹⁰ VINES, Physiology of plants, p. 131. 1886.

The specific conductivity for the aerial stems is higher than that for either leaves or tubers, while the amount of crude ash follows the general law already stated that the amount of ash increases from the roots upwards to the leaves. Repeated determinations of the conductivity of the juice taken from different specimens showed similar results, hence it is evident that the conditions here are different from what was found for *Beta vulgaris*. Considering only the tubers and the leaves, the results again show the conductivity to be a rough estimate of the relative amount of ash; but for the aerial stems the conductivity is higher than it should be if ash alone is concerned. How then is the greater conductivity of the juice from the aerial stems to be explained? It is quite probable that it is due in part at least to the greater amount of organic acids present. Titrations of the juice are extremely difficult on account of the color, even when the juice is considerably diluted, but the titrations made indicated more acid than in either leaves or tubers, which are rather alkaline. This conclusion is also substantiated by the specific conductivity of the ash solution, which is considerably less than obtained for the original juice. The relative amount of ash obtained by Wolff¹¹ for leaves and tubers was slightly different from the above table. His analyses show that the leaves contain nearly three times as much crude ash as the tubers, but a considerable difference was shown by plants taken at different periods in their growth. The different proportions obtained may then be due to the different times and conditions of growth.

3. ALLIUM CEPA.

The juice obtained from both leaves and bulbs was measured with the following results:

	Sp. cond. of juice	Crude ash from 5 ^{cc}	Sp. cond. of ash sol.
Leaves.....	0.0125	0.047	0.00921
Bulb.....	0.00525	0.0229	0.00446

¹¹ WOLFF, Aschenanalysen, p. 75.

The specific conductivity of the juice from the leaves is shown to be more than twice that of the juice from the bulb, and the amount of crude ash obtained from 5^{cc} of the juice follows about the same proportion. The figures for the specific conductivity of the solution made up from the crude ash indicate that the ash alone was not the cause of the conductivity of the juice, but that the organic compounds were concerned. Other determinations were made for this species, and all yielded practically the same results. It may also be noticed that the specific conductivity of the juice from the stalk or stem of a specimen in flower is but slightly in excess of that obtained from the bulb. The relative alkalinity of the ash solution of leaves and bulb is as 2.5 : 1, which is in agreement with the specific conductivity of the solution. The determinations of the specific conductivity of the juice are thus shown in this species to be a rough measure of the relative amounts of ash present.

4. *RAPHANUS SATIVUS*.

For the common garden radish only specific conductivity determinations were made, using the juice obtained from leaves and root. The results obtained from two different specimens will show how nearly the specific conductivities correspond.

	I. Specific cond. of juice	II. Specific cond. of juice
Leaves.....	0.02105	0.02055
Root.....	0.02011	0.01833

The difference here between leaves and roots is less than that obtained for any previous measurements, but the conductivity of the leaf juice is still in excess of that obtained for the root. No ash determinations were made for this species.

5. *NUPHAR ADVENA*.

All of the species used up to this point were taken from places where they had been subjected to about the

same conditions of soil and moisture. It was desirable to make determinations for plants subjected to other conditions, and *Nuphar advena* was selected as a good example of a hydrophyte.

Conductivity measurements and ash determinations were made for the juice obtained from the blades of the leaves, the petioles, the rhizome, and the roots. All parts of the plant used were very carefully washed, and all moisture removed from the surface with filter paper before the juice was extracted. The results obtained are shown in the following table:

	Sp. cond. of juice	Crude ash from 5cc	Sp. cond. ash sol.
Blades of leaves ...	0.009368	0.0328	0.00784
Petioles	0.009368	0.0327	0.00822
Rhizome	0.00761	0.0298	0.00822
Roots	0.006113	0.0226	0.00568

The above measurements show that there is a progressive increase in the conductivity of the juice from the roots through the rhizome to the leaves, the measurements for petioles and blades of leaves yielding the same results. The crude ash determinations show a like progressive increase from the roots upwards. The crude ash was redissolved in distilled water and diluted up to the original volume of the juice, and the specific conductivity of the ash solutions determined. The result obtained for the rhizome ash deviates from what might reasonably be expected, being slightly in excess of that obtained for the juice. The others show a slightly lower conductivity than the original juice, showing that part of the conductivity was due to other than ash constituents.

A comparison may be made of the specific conductivities in this species and some of the previous examples. In *Beta vulgaris* the specific conductivity of the juice from the leaves is

three times as great, in *Raphanus sativus* it is over twice as great, and in *Allium cepa* still in excess, although the difference is not great. The results were what might naturally be expected when we consider the aquatic habitat of Nuphar.

6. CUCUMIS SATIVUS.

For the garden cucumber measurements were made for juice extracted from leaves, stem, and fruit. The roots being small it was not possible to obtain the amount of juice necessary to make the measurements. The results are as follows:

	Sp. cond. of juice	Crude ash from 5 ^{cc}	Sp. cond. ash sol.
Leaves.....	0.0127	0.0621	0.01096
Stem.....	0.0149	0.0609	0.01497
Fruit	0.00632	0.0182	0.00383

This is the only species in which the juice obtained from the fruit was measured, and the examination of fruits of other species is highly desirable. In this instance it will be seen that the specific conductivity found for the fruit is only about half that found for leaves. Here is also another instance in which the specific conductivity of the juice from the stem is greater than that found for the leaves and is not in accord with the amount of crude ash found.

The specific conductivity of the solutions made from the ash of leaves and stem indicates that little besides the ash constituents were responsible for the conductivity of the juice. For the fruit ash, the specific conductivity is but little over half that of the original juice, which indicates that other substances than the ash constituents were concerned. Litmus tests and titrations indicated that the conductivity was produced partly by the acid content of the juice.

7. PORTULACA AND AMARANTUS.

Conductivity measurements were made for two more species, and the results will be given together. In each case roots, stems, and leaves were used with the following results ;

	Portulaca oleracea Sp. cond. of juice	Amarantus retroflexus. Sp. cond. of juice.
Leaves.....	0.02445	0.01711
Stems.....	0.02154	0.01519
Roots.....	0.01069	0.01328

These figures show that for both species there is a progressive increase in the specific conductivity from the roots upward. No ash determinations were made for either of these species.

The results obtained and recorded in the foregoing pages indicate that a method may be afforded of determining the relative amounts of ash in different parts of the same plant. Conductivity determinations of the juice from the same species grown on different kinds of soil would probably yield interesting results. It is known that the ash of any given species varies in amount throughout the period of growth, and it ought to be possible to determine the extent of the variations by means of conductivity measurements. If this is possible, then the much more laborious process of an ash determination would not be necessary.

It may be noted in this connection that there is a difference of potential between the shoot and root of a plant, the root being electro-negative and the shoot in a state of positive electrification. Whether the greater conductivity of the cell sap in the shoot is in any way connected with this condition remains an open question. The facts at least are suggestive.

CONCLUSIONS.

A number of conclusions can be drawn from the foregoing records of conductivity determinations. Although others are indicated, a greater number of species must be examined before

any more definite relations can be established. From the data at hand the following facts seem established :

1. Plant juices are good conductors, and the conductivity is due in large measure to the dissolved mineral substances, while the organic compounds play a minor part.

2. The specific conductivity of the juice obtained from the roots of plants is always considerably less than that of the juice obtained from subaerial parts.

3. The specific conductivity generally increases progressively from the root upward, although in some cases the sap from the stem has a higher conductivity than that from the leaves.

4. In the majority of cases the specific conductivity is a rough measure of the relative amounts of ash present in different parts of the plant.

PARSONS COLLEGE,
Fairfield, Iowa.

ON THE NATURE OF THE STIMULUS CAUSING THE
CHANGE OF FORM AND STRUCTURE IN *PROSERPINACA PALUSTRIS*.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY
XXXVII.

By WILLIAM BURNET MCCALLUM.

(WITH TEN FIGURES)

ALTHOUGH heterophylly in amphibious plants has long been a subject of observation and experiment, as yet we are in ignorance of the real factors that determine which type of leaf such a plant shall assume. The environment of a submerged water plant is certainly a complex one, and there has not been anything like a definite analysis of it. If we are to understand the behavior of a plant when submerged, it is clear that there must be a definite knowledge of the various factors concerned, and of the influence of each one upon the plant. The literature on the subject in the main discusses such topics as water medium, diminished light relations, different oxygen and carbon dioxide conditions, buoyancy, nutrition, and the like; but such terms are general and indefinite, and convey little real information as to the actual factors acting upon the primordial cells of the plant. The demands of physiology can only be satisfied by a detailed analysis of all the possible factors, each of which is a complex in itself, and a determination of the direct action of each resolved component upon the protoplasm of those portions of the plant involved. Of course such an aim is only ideal and at present cannot be realized, but it is, nevertheless, the ultimate goal to be reached before we can read the plant in terms of its environment.

In the hope of obtaining some information upon this question, experiments were begun on *Proserpinaca palustris* in the autumn of 1900, and are still in progress. The plants used have been grown from seed or obtained from the low-lying lands about

Chicago, where they grow abundantly. The work has all been done at the Hull Botanical Laboratory of the University of Chicago, most of the experiments having been carried on in the conservatory. The results are given here only in outline. A



FIG. 1.—Typical air plants, bearing seed.

more detailed account will appear later, when other phases of the work now in progress will be presented.

Proserpinaca palustris grows in low, swampy situations usually flooded in the spring and early summer, and subject to occasional submergence throughout the season. The shoots develop equally well in air and water and present two very distinct forms. When

grown in the air the leaves are lanceolate in outline, 5 to 5.5 cm long and 7 to 8 mm broad, with margins rather finely serrated (*figs. 1 and 3*). The structure is that common to air leaves—that is, thick cuticle, abundance of stomata on the under surface, strong development of palisades, and a well-developed vascular system (*fig. 5*). In the stem there are the usual vascular and mechanical tissues, cortex, etc. The whole form and structure is that of a typical aerial shoot.

When submerged the shoots that develop are entirely different. The leaf is finely dissected, consisting of a slender central rib, with from three to five thread-like lobes on each side (*figs. 2, 4, and 8*), which are often only about 0.2 mm in diameter, and may become 2 cm long. These filamentous divisions are cylindrical in cross-section, and show almost an entire absence of stomata; the epidermal cells are very small

and without any trace of cuticle, the outer walls being thin and delicate (*fig. 6*). There is an absence of any sort of differentiation in the mesophyll, no trace of palisades appearing. The chlorophyll has a marked peripheral placement, the outer cells, which are spherical, being packed full, while the inner ones have almost none. The mesophyll is very loosely arranged, and with a copious development of air chambers throughout. The dry weight is just one-tenth that of the air leaf. There is an entire absence of any sort of mechanical tissue or of xylem, both of

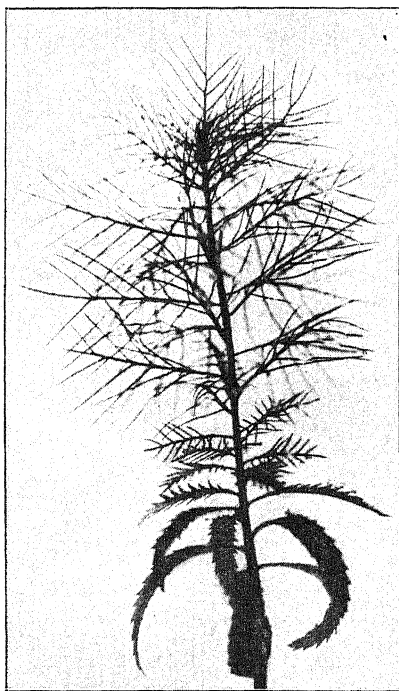


FIG. 2.—Water form in nutrient solution.

which are conspicuous in the air leaves. The vascular system is represented only by a weak development of phloem. The stem of the water form is traversed by large and conspicuous air chambers that connect with the leaves and the roots. The

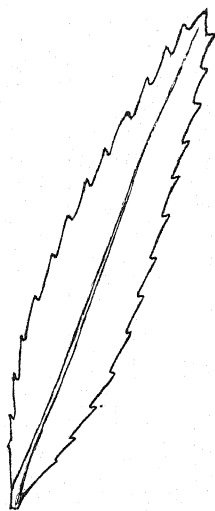


FIG. 3.—Aerial leaf.

mechanical tissue so conspicuous in the air form is absent altogether, nor can any trace of conducting tissue be seen. In the axils, and along the leaf margins, and terminating each lobe, are gland-like structures that possibly function as hydathodes.

No attempt will be made here to give any account of the literature. A good deal of work has been done upon other amphibious plants, but the object of this paper is merely to present some results of experiment on *Proserpinaca*, and the literature will be passed over by merely mentioning a few of the more conspicuous investigations upon the general subject.

Mer¹ considers the aquatic form as due in the main to weakened illumination and nutrition. Constantin² regards it a result of the weakening of vegetative activity. Schenck³ considers it largely a question of the relation to light and to food absorption. Goebel, while recognizing the com-

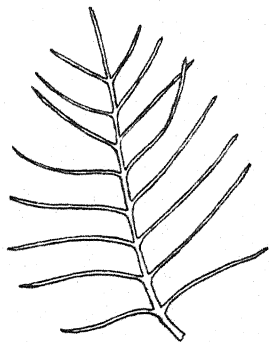


FIG. 4.—Submerged leaf.

¹ MER E., Des causes qui modifient la structure de certain plantes aquatiques végétant dans l'eau. Bull. Soc. Bot. France 27: 194. 1880.

² CONSTANTIN, J., Observations critiques sur l'épiderme des feuilles des végétaux aquatiques. Bull. Soc. Bot. France 32: 83. 1885.

Recherches sur la structure de la tige des plantes aquatiques. Ann. Sci. Nat. Bot. VI. 19: 287-331. pls. 14-17. 1884.

Etudes sur les feuilles des plantes aquatiques. Ann. Sci. Nat. Bot. VII. 3: 94-162. 1886.

³ SCHENCK, Vergleichende Anatomie der submersen Pflanzen. 1886.

plexity⁴ of the conditions, regards light, or rather the lack of light, as the chief factor. Wachter⁵ substantially agrees with Goebel.

There seems to be thus an almost universal tendency among

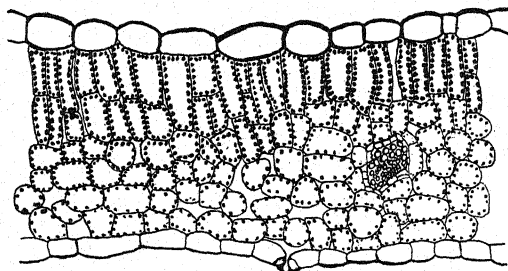


FIG. 5.—Cross section of aerial leaf.

writers to attribute the difference in structure between aerial and water forms to differences in light or nutrition, especially the former. These terms, however, are very general, especially nu-

trition, which involves so much as to mean little in the way of explanation. Ultimately, there must be a critical analysis of the conditions present in the water medium, of the individual factors there that can act upon the growing cells, and the effect of each of these on the behavior of the primordia.

Every living cell in a plant is surrounded at all times by a thin membrane of water through which all substances entering the cell must pass in solution. No substance, be it salt, organic compound, or gas, can enter or leave the cell in any other way than by diffusion as a solute through this film of water. When a plant is submerged this membrane is extended, its thickness

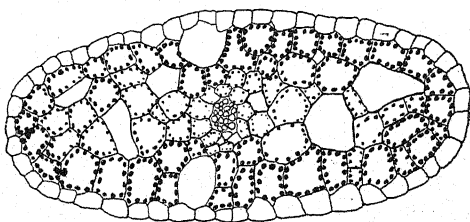


FIG. 6.—Cross section of submerged leaf.

⁴ GOEBEL, K., *Pflanzenbiologische Schildenungen*. Part II. 1891.

Ueber die Entwicklung des Lichtes auf die Gestaltung der Kakteen und anderer Pflanzen. *Flora* 80: 96-116. *figs.* 5. 1895.

Ueber der Einfluss des Lichtes auf die Lestaltung der Kakteen und anderer Pflanzen. *Flora* 82: 1-13. *figs.* 4. 1899.

⁵ WACHTER, W., *Beitrage zur Kenntniss einige Wasserpflanzen*. *Flora* 83: 343-348. 1897.

being the depth beneath the surface of the water; and all gases, etc., and light which reach the cell from the exterior must pass through this increased thickness of water. What different conditions are here introduced, capable of modifying the life-phenomena of the cell? Until we have a definite knowledge of what these conditions are, *i. e.*, of the different physical conditions involving the entrance of gases, salts, or light through water measured by fractions of a millimeter or by centimeters, we cannot hope to know much about the difference in the environment of the cell in air and in water.

Merely for the sake of convenience in discussion, we may arrange what seem to be the possible factors acting upon aquatic plants under the following heads: nutrition, light, temperature, gaseous content of water, substances in the water, and what seems to have altogether escaped notice, the influence of the water itself, either acting as a contact stimulus (stereotropism), or by diluting the cell contents and protoplasm. Of course, such a classification of factors is essentially superficial. It would be quite erroneous, for example, to consider nutrition apart from light which involves photosynthesis, or from temperature, or gas exchange, or absorption of salts; but it will enable us to discuss the matter more systematically and with greater clearness. It is to be understood that the experiments are given here only in outline.

1. LIGHT.—A large number of experiments were conducted. Plants were grown in the strongest sunlight available, and in darkness, and in all stages between, the experiments always being duplicated in water and in air. Plants were also grown in various depths of water. The results were always uniform; the light apparently having no influence whatsoever on the character of the developing shoot. When in the water it produced the water form, and in the air the air form, regardless of the illumination. Plants with their tips the merest fraction of an inch beneath the surface, in both strong and weak light, produced the water form; and those with their tips just above the water produced the air form, no matter what the illumination (*fig. 7*).

These experiments were done many times, with many plants and always with the same result. Objection may be raised that light passing through water is not quite the same as that obtained by shading; and to make sure, plants were grown under double walled bell-jars with the space between the walls filled with water, so that all light coming to the plants had to pass through 2 to 3^{cm} of water. The behavior here was precisely the same as in the other cases, *i. e.*, if the growing tip was in the air, the air form was produced, even when the experiment was conducted in very subdued light. When conducted in bright sunlight the only difference observed was a more



FIG. 7.—Submerged plants in very good and very poor illumination.

vigorous growth. These experiments show that the illumination neither directly, nor indirectly by any subsequent changes that it may involve, can play an essential part in the stimulus to the water form.

2. NUTRITION.—One must hesitate before using this term. It is so very vague and indefinite that its chief advantage lies in its convenience in covering a mass of ignorance. It involves the absorption and the use of oxygen, the absorption of carbon dioxide, and the formation of carbohydrates, and hence the action of illumination; the formation of proteids and hence the absorption of the various salts, also the migration of food and other substances, and all the factors that control this, the toxic and other effects of various ions which may be present. In

fact, the entire list of chemical and physical phenomena occurring within the cell, diverse and complicated as these are, and all the factors which can influence them are involved in nutrition. Disturbances in these nutritive relations may be invoked by the slightest increase or decrease in any of the factors concerned. The change in concentration of a single ion may result in profound changes in the cell. And if the water form of *Proserpinaca* is in any way involved in the nutritive relations it must be because there is some factor, however slight, acting in the water that is not acting in the air.

This we have seen cannot be connected in any way with the light relations. The other possible factors are the relation to temperature, to absorption of salts or ions, to carbon dioxide, or to oxygen. To state, as is not uncommon, that such a phenomenon is due to an increase or decrease of the general nutritive condition of the plant is, of course, merely to say that it is due to a change in one or more of these factors. Experiments were conducted to see what effect these, as they are present in the water, have on the behavior of the plant when submerged.

3. TEMPERATURE.—Most of the experiments were conducted at the ordinary temperature of the conservatory. During the winter some were kept at temperatures so low as almost to inhibit growth, this occurring very slowly. Plants also were kept near the hot water pipes at a temperature so high as occasionally to kill some. In the summer the highest temperatures in the sunlight were used. In all of these cases duplicate experiments were conducted, some in air and some in water, so that the temperature for the two was the same. Some were entirely submerged, some with their tips just above water, some entirely in the air, and some in the air with their tips bent over into the water. In all cases the form of the leaf assumed had no relation to the temperature; as long as any growth occurred the growing points beneath the water produced the water form. In one case two tips at precisely the same temperature were not a centimeter apart, one beneath water and the other above, with all the rest of the plant submerged, and the former produced water leaves,

while the latter developed the air form. In general, the *optimum* temperature for the two forms, so far as could be observed, is about the same. This indicates that temperature, in itself, is not a factor in determining which form shall be produced.

4. SALTS.—The relations of carbon dioxide and oxygen to a



FIG. 8.—Plants after being submerged two months.

possible stimulus will be discussed later under another head, as well as the question of food salts. Plants were grown in distilled water, in tap water, and in nutrient solutions. Some were entirely submerged, with their roots in the soil; others, had the soil washed away from the roots, and shoots and roots submerged in the water. Some in both distilled and tap water were submerged except the very tips, which were in the air. The same was done in various strengths of nutrient solution. All of these were repeated in strong and weak illumination. The results were invariably the same. The finely divided leaf, with the aquatic type of structure in the leaf and shoot, always occurred when the growing tips were submerged, it mattered not whether in distilled water or in nutrient solutions, or in strong or weak illumi-

nation; while when the tips were in the air the broad leaves were produced whether the rest of the plant was in nutrient solution or distilled water. *Fig. 2* shows a plant grown in nutrient solution, and *fig. 8* shows similar plants in water.

This seems to throw out the general conditions of nutrition, so far as the salts are concerned, as having anything at all to do with the production of the air or the water form. The size of the leaf primordia that can be changed from one form to the other may be mentioned here. The oldest leaf primordia that are still folded in the bud average about 6^{mm} in length. There are usually about nine primordia, and they successively decrease in size, the smallest one that can be readily isolated being 0.2^{mm} long. On the creeping shoots there are about eighteen primordia, the smallest being 0.06^{mm} in length. A complete change from the one form of leaf to the other often occurs within four internodes, which means that a primordium may be turned into either an air or a water leaf after it has attained a length of from 3 to 4^{mm} .

5. SALTS, IONS, ETC., AS A STIMULATING CAUSE.—The presence in the water in solution of any such substance as salts, ions, organic acids, or the like, as a stimulating cause to the water form is conceivable. Its possibility, however, is precluded by the fact that the behavior is the same in redistilled water, and to a certain extent in a saturated atmosphere.

6. RELATIONS TO CO_2 AND TO O_2 .—The gaseous content of the water differs from that of the air. The air contains, per $1,000^{\text{cc}}$, 209^{cc} O and 0.04^{cc} CO_2 ; while water at 20°C . contains, per $1,000^{\text{cc}}$, 5.7^{cc} O and 0.3^{cc} CO_2 , about $\frac{1}{3}\frac{1}{7}$ the amount of O, and 75 times the amount of CO_2 . But the rate of diffusion in the water is much slower than in the air, and the cell may be able to use both gases much faster than the slower diffusion will supply them. The leaves cannot be lacking in oxygen during daylight, for the evolution of bubbles of this gas indicates the excess of the amount generated over that used. But the gas will tend to pass off from all surfaces of the cell equally, and as much per unit of surface will pass into the large and numerous air cham-

bers as is given off from the external surface, and the combined surfaces of the former are often greater than the latter. As these air cavities are continuous through the leaf and stem up into the growing parts, it follows from the laws of diffusion that these latter when illuminated must be supplied with an atmosphere rich in oxygen. This internal atmosphere will vary under different conditions, for during the night, or at times when photosynthesis is not active, the excess of O_2 will diffuse out and CO_2 will accumulate. The gas obtained from stems of *Proserpinaca palustris* growing in deep water and after several days of dull weather contained O_2 4.4 per cent., N 35.6 per cent., CO_2 10 per cent.; and the gas removed from the stems of Nuphar during bright sunshine consisted of O_2 35 per cent., N 65 per cent., CO_2 0.6 per cent.

In the case of CO_2 , the slowness of diffusion may counteract the higher percentage in the water. In a perfectly saturated atmosphere, however, where the supply of CO_2 and O is normal, the plant for a long time continues the development of what is essentially the water form. When grown in sugar (lactose) solution the water form is still produced, though in these experiments it has not yet been determined just how much growth has occurred before fermentation has destroyed all the sugar. It is quite possible too that the plant is unable to use the sugar as food.

Plants were grown under water in glass vessels containing atmospheres of different O_2 and CO_2 pressures as follows: (1) one volume of water to an atmosphere containing an equal volume each of CO_2 and O_2 ; (2) one volume water to an atmosphere of three equal volumes of CO_2 and one volume of air; (3) one part by volume of water to three parts by volume of O_2 and one third part CO_2 . For the last experiment the CO_2 pressure was about five hundred times and the O_2 approximately five times as great as that of ordinary atmosphere; while in the second case the O_2 pressure was diminished one-third and the CO_2 pressure increased 250,000 times. In all cases the pressure of the mixture was approximately 760^{mm} mercury; and the

experiments were continued long enough to insure the saturation of the water at these pressures, which in the case of O_2 takes about a couple of weeks.

The results of the experiments were that in every case the water form was produced. This shows that the lack of CO_2 , at



FIG. 9 — Plants grown first in water, then in air, then in water, then in air.

least, cannot be involved in the stimulus to the formation of the water form, for the amount that diffused into the plant was, at least in the one case, certainly greater than that which it gets from the normal atmosphere. Of course it is possible that the large amount might induce abnormal or pathological changes which would prevent the normal development, but the two smaller quantities produced the same results. While an increased pressure of five times the normal O_2 pressure still results in the water form, it is possible that still higher pressure might act differently. This is not probable, however, for two reasons: (1) the plants

during these and other experiments during the day gave off O_2 freely, and this could only occur when the cells are making more than they can use and the protoplasm is supersaturated, probably even more than in the air where the O_2 passes off with less resistance; (2) because of the behavior in moist air where



FIG. 10.—A plant whose upper leaves have developed in saturated air.

the plants have the same amount of oxygen as usual in the atmosphere.

7. MOIST AIR.—The water medium necessarily has the effect of entirely checking transpiration, so that its passage from the cells is entirely prevented, and the cells and protoplasm are filled to their utmost capacity with water. This condition, to a certain extent, can be imitated by growing the plants in an atmosphere saturated with water vapor. Such a thing as a perfectly saturated atmosphere, so far as the plant is concerned, is necessarily impossible, for the temperature of the plant is always slightly higher than that of the surrounding medium, and so evaporation

from it must occur. In a large number of experiments considerable variation in this respect was noticed. Some plants when transferred from the air into a moist chamber showed little change, while others developed leaves somewhat intermediate between those and the water leaves. Some, where extra precaution to keep the atmosphere as near saturation as possible and free from changes of temperature, produced essentially the water form, as in *fig. 10*. The lobes are not so long, but the form is the same. In the case of plants grown from seed in moist chambers, several have reached as many as thirty-five internodes and are still producing water leaves. In these cases the amount of CO_2 and O_2 is the same as if the plants grew in the ordinary atmosphere, so that here, at least, differences in the amount of these gases cannot be any part of the stimulus to the formation of the water form.

The essential feature common to the water and the moist air is the inhibition of transpiration and the consequent choking of the cells and diluting of the protoplasm with water. This can be tested in another way, *i. e.*, by growing the plants entirely under water and at the same time drawing the water out from the protoplasm; or in reality causing evaporation, or transpiration, by means of high osmotic pressure. Plants producing water leaves were placed in nutrient solutions of a strength not quite sufficient to plasmolyze them; also in very dilute solutions made up to the same osmotic pressure with KCl and also $\text{Ca}(\text{NO}_3)_2$. These were allowed to evaporate down, becoming gradually stronger. When they reached a strength of solution equal to about a $\frac{1}{2}$ N salt solution the water leaves ceased to form and the air type of leaf appeared. This shows that even under water, if sufficient water be drawn from the protoplasm, the air leaf will be formed. As the amount of light, CO_2 , and O_2 is the same here as in the water, and the water type is not produced, it is evident that these form no part of the stimulus to the formation of the water form. Further experiments along this line are still in progress, with other salts and also with non-electrolytes.

8. CONTACT STIMULUS.—The young primordia in the submerged plants are intimately surrounded by water, and it is possible that there might be some contact influence here which checks lateral growth and causes the elongation of the lobes. Contact stimulus (stereotropism) is well known among the lower animals, as, for example, where the rhizoids of some of the hydroid polyps develop as a response to a stimulus of contact from a foreign body. That this cannot be the cause, or any essential part of the cause, is shown by the fact of the formation of the water form in moist air, and also from the facts just mentioned, where this contact is present but the air form is produced.

As to the purely anatomical features of the plant, experimental work is being carried on. A large mass of facts regarding the appearance of the various anatomical features under the diverse conditions of experiment has accumulated and will be presented later. One point only need be mentioned. Besides the positive anatomical characters of the water form, there are what we may perhaps term negative characters, *i. e.*, an absence of certain characters that usually accompany the air conditions. These are the absence of such structures as lignified and cuticularized tissues, stomata, mechanical tissue, and conducting tissue. Experiments are under way to determine to what extent such tissues are dependent upon definite external stimulating causes, and to what extent they will respond if these be supplied under the water.

The results of the experiments so far seem to justify the assertion that the stimulus to the development of the water form in the plant under discussion is not involved in the light relations, in the nutritive conditions, temperature, the gaseous content of the water, nor contact stimulus. The only factor which is constant in all cases where the water form develops is the checking of transpiration and the consequent increased amount of water in the protoplasm. When the protoplasm of the primordial cells is in that condition of dilution which accompanies the absorption of a large amount of water, the nature of the

growth and the orientation of the cell division is such as to produce the water form, while those physical and chemical conditions resulting from a partial withdrawal of water by evaporation (*i. e.*, an increased density of the protoplasm) result in that sort of cell behavior which produces the air form of the plant. Just why this difference in the density of the protoplasm should result in such a different behavior of the cells is a question which this paper does not attempt to discuss. The answer can only come with an increased knowledge of the mechanics of cell division, about which at present we know almost nothing.

One other phenomenon must be mentioned. The results given were all obtained from plants collected outside, which were usually producing the air forms, or else from seedlings grown inside. When some of these had been kept submerged it was noticed that after several months they started to produce the air type of leaf. This only occurred in some cases, and even those in the same aquarium behaved differently. Also in the case of those outside, which were submerged all winter, during May and June many of them succeeded in producing air leaves, though none were able to develop flowers. It would seem here as if some of the plants after a time became accustomed to the stimulus and refused to respond. Or it may be that as only the air form is capable of fruiting, in the effort to produce flowers the plant has the ability of self-adjustment to its conditions and develops the air form in spite of its environment. Examination of these primordia showed that the cells are smaller and the protoplasm denser and less distended with water. It is possible that the protoplasm is able to adjust itself, perhaps by the expulsion of water, into that condition in which it exists when in the air. This, of course, is speculation, but investigations are under way, which it is hoped will give us some information on the subject.

In conclusion, I have pleasure in acknowledging my indebtedness to Professor John M. Coulter, Professor Charles R. Barnes, and to Dr. B. E. Livingston, for much kind assistance and advice.

CONTRIBUTIONS TO THE BIOLOGY OF RHIZOBIA.

I. RHIZOBIUM MUTABILE IN ARTIFICIAL CULTURE MEDIA.

ALBERT SCHNEIDER.

(WITH PLATE I)

RECENTLY I began some further work on the biology of rhizobia. The investigations carried on at the Illinois Experiment Station at Champaign in 1893 were terminated before any satisfactory results were reached, and it is only recently that an opportunity has again presented itself to further pursue the investigations.

The review of recent work done in the study of rhizobia will be given in the second paper. A fairly complete list of references up to and including the year 1897 will be found in the *Minnesota Botanical Studies* of September 27, 1894, to which a supplement was added in the *Studies* of May 29, 1897.

Since 1886 numerous investigators, especially those of Germany and France, have attempted to make pure cultures of rhizobia, and some of these have stated repeatedly that cultures were obtained, but not a single investigator has thus far given detailed information regarding them. Other investigators, again, declared that rhizobia were incapable of being grown in artificial media; that they were, indeed, merely plasmic by-products, to which the name *Bakteroiden* was given by Frank and other German investigators. Another source of confusion and difficulty was the fact that most investigators recognized only one form (or species) of rhizobium, namely, the *Rhizobium leguminosarum* of Frank. Without entering again into a discussion of the probable number of species, I shall outline briefly the present preliminary investigations.

I have made repeated attempts to obtain pure cultures of the rhizobia found in the root tubercles of *Melilotus alba*, but with either wholly negative results or only a very evanescent partial success. So frequent were my total failures that I became

almost converted to the opinion that this particular rhizobium was either not an autonomous organism, or that it had lost the ability to grow outside of the host-plant. I have had no difficulty in securing cultures of the rhizobium found in bean-root tubercles, for example, but for reasons which will be given in a subsequent paper I was desirous of obtaining cultures of the comparatively large rod-shaped to Y-shaped form found in sweet clover. For some time after beginning the present series of experiments it appeared that my efforts would again be without positive results; but my former experiences induced me to proceed more cautiously and more carefully, keeping in mind the probable physiological peculiarities of this particular rhizobium as compared with bacteria in general. Now I feel certain that in 1893 I had several small pure cultures of this particular rhizobium, but failed to recognize them, and they were destroyed without being investigated, and, unfortunately, I was furthermore obliged to discontinue the investigations at a time when I was becoming somewhat familiar with my subject.

In the following experiments young seed-grown plants of *Melilotus alba* were selected, which were about four inches high, each plant having from six to fourteen fairly well developed, mostly single, non-branching, more or less irregularly oval to flattened tubercles. The roots and tubercles were thoroughly and repeatedly washed in hydrant water, and dried with blotting paper. A tubercle was cut into with a small sterilized knife, and the knife-blade was lifted, thus breaking the tubercle across. This prevented the blade from dragging exterior bacteria over the interior of the tubercle. A short platinum needle was pushed into the central portion of the tubercle and streak (line) cultures made in Petri dishes with *Melilotus alba* extract solidified by means of agar. The inoculated Petri dishes were kept in the dark at the spring and early summer temperature of the laboratory. Most of the dishes showed white growths in a day or two. Examination proved these to consist of several motile bacteria, including a large motile bacillus resembling *B. anthracis* or *B. subtilis*. In the course of about five days from the time of

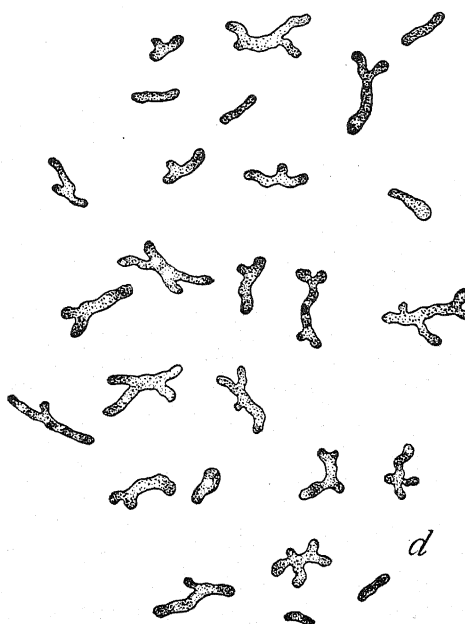
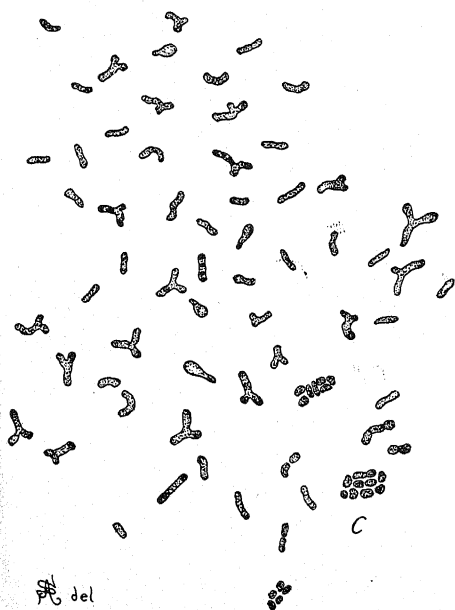
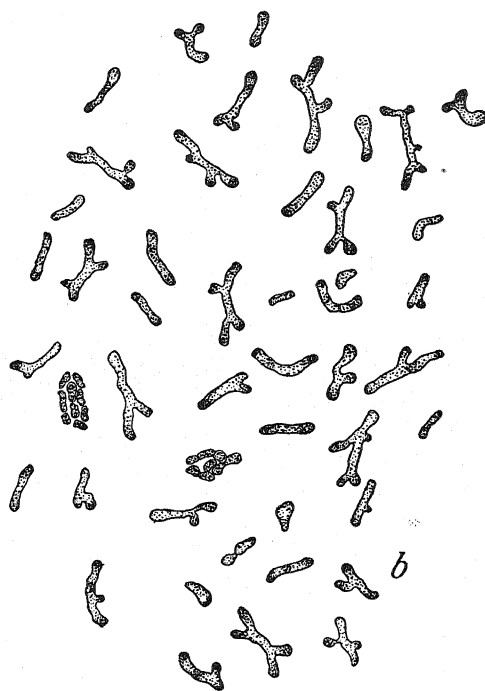
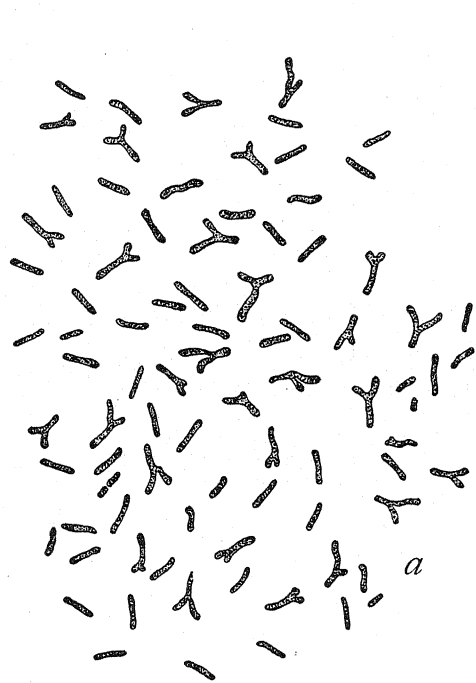
making the inoculations I noticed in several of the streaks a very slight, translucent, glistening growth, which at once reminded me of similar growths observed in my former investigations. Upon microscopic examination I found numerous organisms, some simple and irregular in form, some Y-shaped, some twice and three times forked, resembling the rhizobium of the sweet clover to which I gave the name *Rhizobium mutabile* in 1892. Of these few small growths I made a number of test-tube cultures. These cultures developed very slowly, but steadily, producing (upon agar media) a transparent, glistening, slightly elevated, smooth-margined growth of about the tenacity (not stringy) and consistency of syrup. There was no color, odor, or gas formation noticeable. Repeated microscopic examinations showed these cultures to consist of organisms having the morphological characteristics of *R. mutabile* of sweet clover. These morphological characteristics, combined with the very peculiar development of the cultures, led me to assume that I had at last succeeded in obtaining pure cultures of *R. mutabile*. H. B. Carey, working in the same laboratory, succeeded in obtaining numerous similar cultures from *M. alba* tubercles by the fractional culture method. The evidence, though requiring further proof, is sufficient to justify this report. Inoculation experiments on *M. alba* growing in carefully sterilized soil are now in progress, which will be reported upon in the second paper.

Microscopic examination of pure cultures showed the rhizobia in various stages of septation, budding, and branching. The organisms are absolutely non-motile, showing more irregularity in form, size, and branching than in their normal state within the tubercle. They are embedded in a considerable quantity of mucilaginous substance, which does not, however, form a distinctly circumscribed layer about the cell wall. Naturally the study of the mode of multiplication is a comparatively easy task with pure cultures. It multiplies by bi-septation, multi-septation, and by budding and subsequent septation. In comparatively rare instances there is evidence of budding resembling that of

the yeast plant. Growth is usually uniterminal; again it may proceed in either direction or toward all of the extremities of the branching forms, until the maximum size is reached, whereupon it septates. Under favorable conditions, when food supply is adequate, septation proceeds more rapidly and before the maximum size is attained, forming zoöglœa of only partially developed rhizobia. When a fully matured organism septates, the cytoplasm collects into two, more generally three to five, masses, followed by a constriction of the cell-wall between the plasmic masses. Branching forms seem to be due to arrested, prolonged, or incomplete budding, and occur principally in the older, more mature plants, though it may also be noticeable in immature or undeveloped organisms. These peculiarities of form and budding indicate a relationship to *Saccharomyces*, but there are absolutely no fermentation phenomena in the media.

In the older, larger, and more matured cells are found those small, usually spheroidal, highly refractive bodies to which attention has been called by various investigators, notably Frank. In the culture organisms, as well as in those found in tubercles, these bodies, which vary in number from one to five, usually occupy a peripheral position. They are highly refractive, in that respect resembling spores. In 1894 I described them as modified spores, an opinion not seconded by Frank (a communication in writing). At present I have nothing to add regarding their origin and probable function, though I am still of the opinion that they may be spore-like etiologically, and might be designated sporoids. It seems evident that no true spores are formed, either in the organisms of the tubercles or those grown in media.

Rhizobium mutabile grows in most media, liquid beef broth gelatine, agar, beef broth, whether neutral, slightly acid or slightly alkaline. It seems to grow better upon solid than in liquid media. It grows best, as far as observations have been made, upon solid *M. alba* extract agar. It is not anaerobic, though it may be facultatively so. The fact that the culture is colorless renders the study of deep stab growths difficult,



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SCHNEIDER on RHIZOBIUM MUTABILE

especially if the media are not wholly translucent or transparent. In liquid media there is a whitish sediment of rhizobia. There is evidence that growths on solid media become less translucent with age.

The following is a brief summary of results of the present series of experiments:

1. *Rhizobium mutabile* can be isolated and develops in artificial culture media, forming a translucent, colorless, glistening, semi-liquid growth.

2. It develops slowly, requiring from four to six days to produce a perceptible growth.

3. It is essentially aerobic.

4. It multiplies by biseptation, multiseptation, and a modified form of budding.

5. It apparently does not develop true spores.

6. It is devoid of all active motion.

7. It undergoes great changes of form and size, with age and also in different culture media. See figures.

8. Refractive bodies (sporoids) occur in the older organisms, and seem to be characteristic of the species. Their origin and function are as yet undetermined.

9. While of slow growth, it does not seem to be readily destroyed. It may be completely overspread by a foreign germ, but as soon as conditions become unfavorable for the latter the rhizobium is found to be still active and continues to grow and multiply.

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EXPLANATION OF PLATE I.

The illustrations are from pen and ink drawings, made on a uniform scale by means of an Abbé camera lucida. The drawing paper was placed on a level with the base of a Leitz instrument. Magnification by means of a B. and L. 1-12 oil immersion objective and a No. 4 Leitz ocular, draw-tube in.

a, *Rhizobium mutabile* from young root tubercle of *Melilotus alba*.

b, *R. mutabile* grown in agar beef broth.

c, *R. mutabile* grown in beef broth.

d, *R. mutabile* grown in *Melilotus alba* extract solidified by agar.

NOTES ON CERTAIN SPECIES OF ANTENNARIA.

ELIAS NELSON.

CONSIDERABLE attention during recent years has been given to the study of the eastern species of *Antennaria*. Many species of the middle Atlantic states and of the prairie states of the Mississippi valley have been characterized by Professor E. L. Greene, those of the District of Columbia and vicinity in particular having been the subject of much field study by the same author. Mr. M. L. Fernald has published a synopsis of the New England species, supplemented by subsequent papers containing notes and a key. Through the field and herbarium studies of Mr. Fernald, and the notes and observations of various collectors, the species of the New England states are perhaps better known than those of any other region of equal area in North America. The most recent synopsis of the eastern species is that which has appeared in Dr. Britton's *Manual*. Thanks to the efforts of many collectors, we are constantly becoming better acquainted with these plants, but much remains to be learned even concerning the eastern species.

A revival of interest in any long neglected group of plants, is generally attended with much describing of species, resulting in many new names, some of which must sooner or later be relegated to synonymy. It is not at all surprising, therefore, to find that several of the species now generally accepted have received two or more names during the recent study of this genus. What in many instances appeared to be very distinct, on further examination in the light of more material often proves to be less deserving of the specific or perhaps sub-specific recognition at first accorded it. A fair representation of a species by specimens from different localities in its range is necessary for an adequate knowledge of the plant. The variations, relationship, and distribution of each species needs to be worked out, and as

regards our eastern *Antennarias* this remains to be done for most of them.

The plantain-leaved species are very polymorphous and almost indistinguishable. It would not be at all difficult in any large collection to spread out a series of specimens exhibiting a gradation of *A. neglecta* through *A. petaloidea* and *A. ambigens* into *A. Parlinii*. In spite of the frequent intergradations we do recognize as tolerably well marked some categories of forms to which it seems proper as well as desirable to assign binomial names. Though authors will to some extent differ in judgment as to the validity of certain species, it is gratifying to note that different investigators in this group in several instances have reached the same conclusions.

In the segregates of *A. plantaginifolia*, *A. dioica*, and *A. alpina* of earlier American authors, the general habit and stature of the plant, the outline and size of the leaves, the character and permanency of the pubescence, and the height of the involucre are of most value for specific diagnoses. The outline of the bracts of the pistillate involucre, especially as regards the bluntness or acuteness of their tips, are of minor importance in distinguishing species. In most of the eastern as well as of the western *Antennarias* I have found that the tips of the involucral bracts (pistillate) vary from obtuse to acute or acuminate. The outline of the bracts has quite generally been given in recent descriptions, and the bluntness or acuteness of their tips has in many instances been taken as one of the distinctive characters of certain species and sub-species. The amount of thickening or dilation of the pappus bristles of the staminate flowers is also found to be subject to considerable variation in the same species.

It is a well established fact that parthenogenesis occurs in the real *Antennaria alpina*. While there is at present no evidence to show that any North American species are propagated parthenogenetically, it perhaps would not be at all surprising to find that it does take place in some of them. We at least know that good seeds may be produced. Mr. Theo Holm, of Brookland, D. C., assures me that he has observed in that vicinity an abun-

dance of seedlings, but which species they represented could not be determined. They were found, however, near patches in which *A. Parlinii* (*A. arnoglossa*), *A. plantaginifolia*, and *A. neglecta* were growing. In *Antennaria*, as well as in the related genera *Gnaphalium* and *Anaphalis*, the plants may be polygamo-dioecious. *A. plantaginifolia* (*A. decipiens* Greene), however, is the only species in which I have observed perfect flowers.

In consequence of my distribution of North American *Antennarias* I have received many collections from various parts of the United States and Canada, thus giving me an opportunity to study among others the species of the eastern United States. The material in the U. S. National Herbarium has been at my disposal, and through the courtesy of Professor E. L. Greene it has been my privilege to examine the types of his species. I am under great obligations to Mr. M. L. Fernald for communications of specimens and other favors. The facts which have been brought out in the course of my study of the eastern species and the opinions I have been constrained to entertain are set forth in the following notes, which I hope will not be without interest to the students of this genus.

ANTENNARIA LABRADORICA Nutt. Trans. Am. Phil. Soc. 7:406. 1841.—A very good species, originally described from Labrador specimens. It is in part the *A. alpina* of Britton's *Manual*. There can be no doubt as to its distinctness from *A. alpina*. Nuttall himself says of it: "at first glance resembling *A. alpina*, but more nearly allied to *A. plantaginea*." Its affinities are with *A. canadensis* and *A. neodioica*, the brownish involucres suggesting *A. alpina*. I have examined an undoubted specimen of this species deposited in the herbarium of the Geological Survey of Canada (sheet no. 14363). Since Professor Greene, who has seen the same material, gives a brief characterization of the species,¹ I will here only record some measurements taken of some parts of the plants on this sheet. Basal leaves 1–2^{cm} long; lowest pedicel of the inflorescence 3.5^{cm} long; involucres 6–7^{mm} high.

¹ Pittonia 3:285. 1897.

ANTENNARIA NEODIOICA Greene, Pittonia 3:184. 1897.—*A. neodioica attenuata* Fernald, Proc. Bost. Soc. Nat. Hist. 28:245. 1898. *A. rupicola* Fernald, Rhodora 1:74. 1899. *A. alsinoides* Greene, Pittonia 4:83. 1899.—This species was described from specimens secured near Stroudsburg and Bushkill in the extreme eastern part of Pennsylvania. Typically it has involucre whose outer bracts are obtuse and the inner acute. True *A. neodioica* is much less common than the forms with narrow, attenuate involucre bracts. The staminate plants are certainly very rare, being unknown both to Mr. Fernald and myself. Professor Greene, however, seems to have had some staminate plants when drawing up the original description.

Taken in its entirety, this species is readily separated from any *Antennaria* to be found in eastern North America. It is quite variable, and some of its forms have received sub-specific or even specific names. Dr. Britton² considers all the forms of this particular category as representing only one species. In this I think he is entirely right. I had myself, independently, reached the conclusion that *A. neodioica attenuata* and *A. alsinoides* are the same, and am now of the opinion that the form to which these two names were applied cannot consistently be accorded even sub-specific rank.

An examination of a series of specimens from localities ranging from Ontario and the New England states to Maryland shows that the species varies chiefly as follows: basal leaves from relatively narrow with oblanceolate expanded portion and then not clearly differentiated into blade and petiole, to rather broad, the expanded portion obovate with a more distinct petiolar base; inflorescence from somewhat paniculate to subcorymbose, either closely congested or tolerably open; bracts from much acuminate to more or less obtuse, scarious or petaloid, rarely lemon-tinged. Were any two or more of these variations always associated, there would here be some justification in recognizing sub-species. Professor Greene states that his *A. alsinoides* as compared with the typical *A. neodioica* has its heads

² Science, n. s. 13:587, 1901.

on shorter pedicels, and that its leaves are more "clearly differentiated into blade and petiole," the expanded portion of the leaves being obovate. The congested character of an inflorescence is found to be by no means always accompanied by relatively broad leaves, for some Ontario specimens examined by me have an inflorescence answering to Professor Green's description, but the expanded portion of the leaf is oblanceolate. The stolons are said to be equally leafy throughout, but that is quite often the case in typical *A. neodioica*. Mr. Fernald assigns to his *A. neodioica attenuata* no other distinctive characteristic than that exhibited by its involucral bracts. It does not seem well to make sub-species on single characters, especially of a species with such freely intergrading forms. The character of attenuate bracts is accompanied either by relatively narrow or rather broad leaves, and either by a close or tolerably open inflorescence. Mr. Fernald has characterized another sub-species, viz., *A. neodioica grandis*, of which I have seen no specimens. *A. rupicola* is merely a dwarfish form of *A. neodioica*, with lemon-tinged involucral bracts and basal leaves slightly narrower than is ordinarily the case in this species.

ANTENNARIA PETALOIDEA Fernald, *Rhodora* 1:73. 1899.—*A. neodioica petaloidea* Fernald, *Proc. Bost. Soc. Nat. Hist.* 28:245. Je 1898. *A. neglecta subcorymbosa* Fernald, *l. c.*, 246. *A. Farwellii* Greene, *Pittonia* 3:347. S 1898. *A. petaloidea scariosa* Fernald, *Rhodora*, *l. c.* *A. petaloidea modesta* Elias Nelson, *Proc. U. S. Nat. Mus.* 23:710. 1901.—In this species we have a connecting link between the unusually well marked *A. neglecta* and *A. ambigens*. Though grading into *A. neglecta* it may be distinguished readily from that by its corymbosely cymose inflorescence and generally broader leaves. The heads are as a rule more numerous than in *A. neglecta*. In that species, as noted by Mr. Fernald, the staminate plant is quite as common as the pistillate, while in this it is very rare. As in *A. neglecta*, the thin tomentum of the upper surface of the leaves is either persistent or deciduous. In outline the leaves vary from spatulate or oblanceolate to obovate-cuneate, and in width from 7 to 17^{mm}.

The stolons, though generally like those of *A. neglecta*, are often more leafy, and then resemble those of *A. ambigens*. *A. petaloidea*, when constituted as a species by Mr. Fernald, was known to him only from northern New England. I have it, however, from two localities in Ontario, and Mr. C. K. Dodge has collected it repeatedly in St. Clair co., Mich. Undoubted specimens of this species have also been secured by Professor De Alton Saunders in the Black hills of South Dakota. This collection contains both pistillate and staminate plants. The latter are 8-13^{cm} high, with two to four heads to the cluster, the bracts with oval to oblong, obtuse tips, and the pappus bristles with moderately and uniformly thickened upper portions, or occasionally very slightly dilated at summit.

I have examined the type of *A. Farwellii*, and find that it is nothing else than *A. petaloidea* Fernald. What Mr. Fernald³ and Dr. Britton⁴ have supposed to be *A. Farwellii* is not that species, but a much larger-leaved plant closely allied to *A. ambigens*. The basal leaves in the type are lightly tomentose above, indistinctly 3-nerved beneath, only 3-4^{cm} long, and not exceeding 13^{mm} in width.

ANTENNARIA PARLINII Fernald, Gard. & For. 10: 284. 1897.—*A. arnoglossa* Greene, Pittonia 3: 318. 1898. *A. Parlinii arnoglossa* (Greene) Fernald, Proc. Bost. Soc. Nat. Hist. 28: 243. 1898.—The typical form of this species is a New England plant with leaves green and glabrous above from the first, with stems beset with purplish ciliate hairs and with large involucre of narrow acuminate inner bracts. There are some deviations from this type even in the New England states. The ciliate hairs are at times absent, and the basal leaves often slightly arachnoid above. Some Illinois specimens examined by me are also somewhat arachnoid on the upper surfaces of the leaves, and very few ciliate hairs are present. In plants from Washington, D. C., and vicinity the ciliate hairs are present in some, absent in others, the leaves either wholly glabrous above or nearly so and the involucre bracts either broad and obtuse or rather narrow. It

³ Rhodora 1: 153. 1899.

⁴ Manual, 976.

will be seen from the above account of its forms that as to involuclral bracts, glandulosity, and presence of ciliate hairs it presents the same variations as *A. ambigens*. As to stature, size of leaves and involuclres, and general habit it resembles that species very closely and indeed it grades into it. Although there is no sharp line of demarcation between these two species, yet it seems well to let the two names *A. ambigens* and *A. Parlinii* stand for the two categories of forms, those with permanently tomentose upper surfaces of the leaves falling into the former, and those with leaves smooth above or nearly so into the latter. From *A. plantaginifolia* the species is quite readily separated, and though the chief distinction is that of size the difference is constant, and I think no one who once has formed a mental picture of the two species would have any difficulty in distinguishing them.

ANTENNARIA PROPINQUA Greene, Pittonia 4: 83. 1899.—Originally described from staminate specimens only, collected at Harper's ferry, West Virginia, but now also known to me through plants secured by G. B. Ashcraft at Berea, Ohio. This collection contains both staminate and pistillate specimens. Even the pistillate plants are rather low, only 16^{cm} high; the heads few and closely congested, and the involuclres 8^{mm} high. The herbaceous portion of the involuclral bracts is livid green and glandular. The inner bracts of the pistillate involuclres are narrow and acuminate, while the outer are somewhat broader, their tips oblong, lanceolate, or oblong-linear, acute or obtusish. The pappus bristles in the staminate flowers are only slightly narrower at the tips than those observed in some specimens of *A. Parlinii*. When more specimens of *A. propinqua* are at hand, we shall be able to judge better of its claims to specific rank.

ANTENNARIA BRAINERDII Fernald, Rhodora 1: 153. 1899.—It is doubtful whether this can be maintained as a distinct species. As exemplified by Mr. W. W. Eggleston's specimens of 1899 and President Brainerd's of 1900, it is certainly very closely allied to *A. Parlinii* on the one hand and to *A. ambigens* on the other. In both of those species, as we have already noted, the presence or absence of ciliate hairs is a matter of much variation, and in

both the basal leaves are at times relatively as broad as those of *A. Brainerdii*.

ANTENNARIA AMBIGENS (Greene) Fernald, Rhodora 1: 150. 1899.—*A. arnoglossa ambigens* Greene, Pittonia 3: 320. 1898. *A. Parlinii ambigens* (Greene) Fernald, Proc. Bost. Soc. Nat. Hist. 28: 244. 1898. *A. fallax* Greene, Pittonia 3: 321. 1898.—This is the commonest of the eastern species of *Antennaria* which have large heads and ample, plantain-like basal leaves. It ranges from Minnesota, Ontario, and Maine to Kansas, Mississippi, and Virginia. As many other American species, it is quite variable. It is nearly always more or less glandular, quite as often so in the acuminate-bracted forms as in the typical one. Ciliate hairs may be found about the inflorescence, on the stems, and on the margins and surfaces of the leaves. These hairs are usually purple, but when occurring on the surfaces of the leaves are colorless. The upper surfaces of the basal leaves are permanently arachnoid or tomentose above, and the tomentum of their lower surfaces is generally persistent. Often, however, it forms a crustaceous coating which occasionally is deciduous in flakes. The involucre bracts of the pistillate plants may be either narrow and attenuate or broader and petaloid. Often they are purplish as in *A. Parlinii*. There is some variation in the stature of the plant, the leafiness of the stems, and the character of the inflorescence, but these variations fail to furnish any diagnostic characters. The staminate plant is somewhat lower and its involucre bracts have ovate or oblong, obtuse, petaloid tips. The pappus bristles are either clavellate or more or less dilated and then bluntly toothed or somewhat lacerate, the filamentous portion serrulate upwards.

The type specimens of *A. arnoglossa ambigens* were collected near Brookland, D. C., and Professor Greene informs me that he has found but one patch of it and that situated in a field of his *A. fallax*. These specimens are slightly glandular and the tips of the outer involucre bracts are oblong and obtuse, those of the inner acuminate. On one of the sheets the plants have some purple hairs about the inflorescence.

The type material of *A. fallax* was collected in the same locality as that of *A. arnoglossa ambigens*. There are six sheets labeled *A. fallax* in the herbarium of Professor Greene. On three of the sheets the plants are without ciliate hairs, while on the other specimens these are present. Only two of the four specimens of pistillate plants have attenuate inner bracts, and in only one of these are they setaceously pointed. One of these specimens with inner attenuate bracts has some purple hairs about the inflorescence.

There is thus a very evident gradation of *A. arnoglossa ambigens* into *A. fallax*, even in the original material. A careful study of a larger series of specimens shows that the two cannot be separated, being simply forms of one species. I have recently learned through a communication from Mr. Fernald that further observation in the field has led him to the same conclusion, and Dr. Britton⁵ also is inclined toward this belief.

ANTENNARIA PLANTAGINIFOLIA (L.) Rich. in Hook. Fl. Bor. Am. 1: 330. 1837.—*Gnaphalium plantaginifolium* L. Sp. Pl. 850. 1753. *G. plantaginea* L. Syst. Veg. Ed. 12. 2: 545. 1767. *A. plantaginea* (L.) R. Br., Trans. Linn. Soc. 12: 123. 1818. *A. decipiens* Greene, Pittonia 3: 278. 1898.—*A. nemoralis* Greene, Pittonia 4: 41. 1899. This is the low, plantain-leaved species, having small heads and foliage persistently arachnoid on the upper surface. It is closely allied to *A. ambigens* and grades into it. It is a comparatively glandless plant, the flowering stems and the leaves being rarely at all glandular, and in no specimens have I detected any ciliate hairs. The basal leaves vary from round obovate to ovate or narrowly elliptic, and the petiole is often much elongated, especially in the forms with narrower leaves. The bracts of the pistillate involucre are generally petaloid and obtuse or obtusish, but not infrequently somewhat scarious and acute or acuminate in the inner. In the staminate involucre the whitish tips are oval, ovate, or oblong, and vary in different plants as to size and number. The pappus bristles in the staminate flowers though generally very narrow

⁵ Manual, p. 796.

and serrulate are at times somewhat dilated toward their apices.

I am unable to separate *A. nemoralis* Greene from this species. It is of the same size and has the same foliage characteristics as *A. plantaginifolia*. Mr. Albert Ruth has sent me some material secured by him in the same grove in which was collected the type of *A. nemoralis*. The leaves in these plants vary from ovate and elliptic to round ovate, and the arachnoid pubescence is persistent on the upper surface. There were two pistillate plants in Mr. Ruth's collection, and these have the narrow involucre bracts characteristic of *A. plantaginifolia*.

Hermaphrodite flowers apparently are not infrequent in this species. Plants with some flowers containing well developed stamens and pistils and plump akenes have been detected in three different collections. These specimens are respectively from Biltmore, North Carolina, Takoma park, D. C. (*E. N. Wilcox*, 1901), and Knoxville, Tennessee (*Albert Ruth*, 1901). They are in each case accompanied by sterile plants. They are readily distinguished from both the strictly pistillate and the staminate individuals by their involucre bracts, which are much broader than in the former, but not as broad as in the latter; or, to be more definite, their obtuse, white tips are from oblong-linear to oblong. The pappus-bristles are coarser than those of the pistillate flowers, slightly thicker toward their apices and somewhat serrulate. In their general appearance the heads of the individuals having some perfect flowers resemble those which are strictly pistillate, and indeed I at first mistook them for pistillate plants.

ANTENNARIA OCCIDENTALIS Greene, Pittonia 3: 322. 1898.—The plant which I at present tentatively refer to *A. occidentalis* is the *A. Farwellii* of Mr. Fernald and Dr. Britton. It appears to be quite distinct, and is known to me through specimens from New York, Vermont, Ontario, Michigan, and Wisconsin. As to the involucre and the outline of the basal leaves, it agrees so well with Professor Greene's description of *A. occidentalis* that I refrain from assigning it a new name until satisfied that it is not that species.

ANTENNARIA ARGENTEA aberrans, subsp. nov.—Like the species, but inflorescence racemosely paniculate.—Type in the U. S. National Herbarium, collected by M. E. Jones on Mt. Shasta in California, alt. 5,000 ft., June 18, 1897. There are only pistillate plants on the sheet, and these are about 15^{cm} high, and have oblanceolate, acute radical leaves 3-4^{cm} long and 6-7^{mm} wide.

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A SURVEY OF THE HURON RIVER VALLEY.

I. THE ECOLOGY OF A GLACIAL LAKE.

HOWARD S. REED.

(WITH FOUR FIGURES)

I. INTRODUCTION.

IN the vicinity of Ann Arbor, Mich., there are a number of glacial lakes and ponds which at no very distant day must disappear if the processes now in operation continue. At present they exhibit conditions of such interest that it has seemed very desirable to preserve as complete a record as possible of their extent, physical characters, and biological relations as they exist today. The work here reported was carried on at the largest of the so-called "Sister lakes" west of Ann Arbor.¹ It was undertaken at the suggestion of Professor V. M. Spalding, of the University of Michigan, under whose direction the botanical survey of which it forms a part is now in progress. It has been the purpose of the writer to give an exact representation of existing facts and conditions, and to study in a somewhat quantitative manner the relative value of the several ecological processes at work; necessarily some matters of theoretical interest are discussed.

The study of a glacial lake is of peculiar interest to students of ecology. The physiography of the country in which such lakes occur was entirely rejuvenated by the glacial action, and the physiographic processes taking place now are precisely those rapid developments characteristic of new land areas. Adaptations to past conditions still remain, but with them are striking and interesting adaptations to present changing conditions. The general change has been from semi-arctic and hydrophytic to temperate and mesophytic conditions. At the same time, there

¹ A preliminary report of this work was published in the Proceedings of the Michigan Academy of Science for 1901.

has been a continuous reaction of plant life upon environment; the advancing zones leave soils behind them different from those they found. Sphagnum swamps and peat bogs, into which the lakes now under consideration are changing, are the last stages in the life history of glacial lakes.

The plant life of the small glacial lakes characteristic of southern Michigan differs distinctly from most other hydrophytic societies. It is predominantly xerophil, while that of a brook or river is predominantly hydrophil in character.² It differs from the flora of such lakes as have been studied by MacMillan³ and Pieters⁴ in not being influenced by waves, currents, spray, etc.

II. GEOLOGICAL HISTORY.

The lake selected for study is a "kettle-hole" in the terminal moraine which formed part of the northwestern shore of ancient Lake Maumee. It is mainly fed by springs issuing from the bottom and around the shores, though a small rivulet entering from the southeast contributes some surface water during about half the year. The lake probably came into existence at the close of the second advance of the ice sheet, and at that time it was considerably larger than at present, due to the drainage from the melting ice. For some time following the formation of the lake it was apparently subject to sudden changes in size and outline due to rapid fluctuations in the water supply. There are two similar lakes within a mile to the eastward, with which it formerly may have been continuous; at present the surface of the water is five inches lower than in either of the other two lakes.

The original lake must have been from sixty to eighty feet deep in its deeper parts, and the surplus waters were discharged through an outlet to the southwest which emptied into the Huron river. The eastern shore was fifteen or twenty rods farther east than at present; while from the southeast a wide

² COWLES, H. C., BOT. GAZ. 31: 145. 1901.

³ MACMILLAN, C., Minnesota Botanical Studies, 50.

⁴ PIETERS, A. J., U. S. Fish Com. Bull., pp. 57-79. 1901.

cape extended into the lake, which now appears as a hill near its southeastern corner. West and southwest of this cape the water's edge was about twenty rods back of its present position, and the former western margin was approximately parallel to the present one, but four or five rods farther inland. A shallow bay extended off toward the northwest, which is still traceable by the extension of plant zones in that direction. On account of the steepness of the northern shore, the water on that side extended only a few rods beyond its present limit.

This former extension of the lake has had a marked influence upon the present plant societies. While it prevailed it necessarily drowned out all terrestrial forms; then as the water level slowly fell the aquatic and semi-aquatic species had the first chance to get a foothold and become established upon the land which was thus gradually uncovered. This was especially the case on the east, west, and southwest shores of the lake, where, on account of the gentle slope of the bottom, there was always a wide strip of shallow water in which aquatics and semi-aquatics could get a strong foothold and become established long before it was suitable for the occupation of terrestrial forms. Even today the zone of willows is destitute of any considerable number of distinctly terrestrial plants.

At a certain stage in the recent geological history of the region, as the water level fell, the large lake was divided into two, the present lake and a similar, smaller one ten rods south of it which has all but disappeared. The fate of this smaller lake throws some light on the history of the present lake, as will be shown later.

III. PRESENT CONDITIONS.

I. *PHYSIOGRAPHIC RELATIONS.*—As it now exists, the extreme east and west diameter of the lake is a little more than thirteen hundred feet long, the extreme north and south diameter is seven hundred feet. Between the water's edge and the higher ground which formerly constituted the shores is a swampy border varying in width from ten feet to twenty rods. The thick growth of vegetation in this border has nearly clogged the

sluggish outlet at the southwestern corner of the lake. The border swamp is interrupted on the south side of the lake by the former delta of the brook entering at that place. The delta rises several feet above the level of the surrounding shore and differs from it very markedly in vegetation (*fig. 1*).

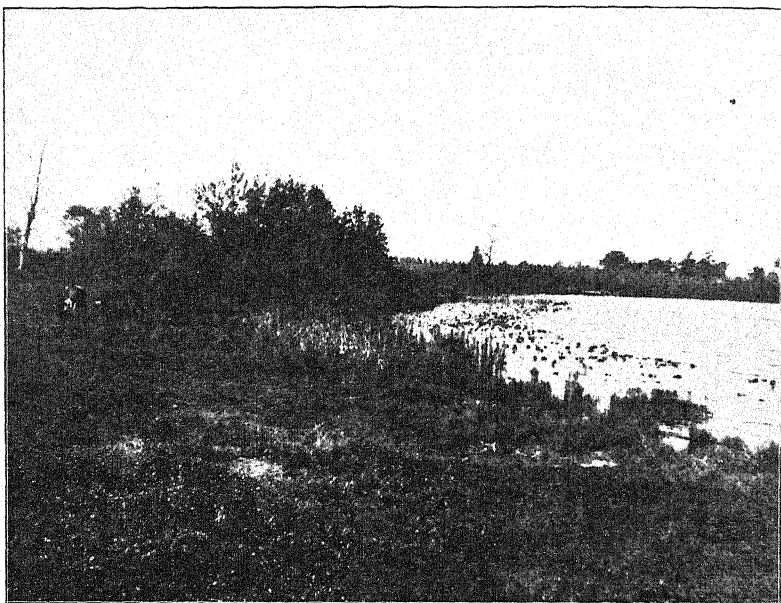


FIG. 1.—South shore of the lake, part of the former delta plain in the foreground.

The lake basin proper is surrounded by a shallow marginal rim varying from forty to seventy-five feet in width and descending from the water's edge at one side to eighteen or twenty feet below the surface at the other. This marginal rim owes its existence primarily to organic factors which are still at work modifying and extending it. The soil for several feet in depth is largely composed of organic material which presents the usual successive gradations from vegetable detritus to muck and peat. The bottom descends very rapidly from this rim to form the main central basin, which averages more than fifty feet in

depth. The soil of the central basin is almost pure loess-like clay mixed with a little fine vegetable detritus which settles from the water of the lake; this area, so far as numerous dredgings show, is entirely barren of vegetable life of any kind.

The water of the lake enters chiefly by underground channels and from springs at the bases of the gravel hills surrounding the lake. During the greater part of the year the supply is just about equal to the loss by evaporation, and except during seasons of maximum precipitation there is very little water passing into the outlet. The water dissolves and holds in solution so much organic substance from the decaying vegetation in the lake that a very perceptible taste is imparted to it. The fine detritus held in suspension together with the dissolved substance renders the water brownish, making it impossible to distinguish objects more than six feet below the surface. The opacity of the water is an important factor in determining the distribution of plants. Obviously there are no perceptible currents in so small a lake.

2. THE PLANT SOCIETIES.—The deep central portion of the lake does not, so far as could be ascertained by dredging, support any plant life; this cannot be due to the soil, for in other lakes the same soil is covered with *Chara* and *Potamogeton*, but is undoubtedly due to the feeble intensity of light at depths greater than twenty feet.

The plants at the lake are grouped in five fairly well defined concentric zones, occupying all the suitable lake bottom less than twenty feet under water, and all the land surrounding the lake which feels the influence of the presence of the water. Beginning with the innermost, they are:

(a) *A zone of Potamogeton*, which extends in water from eighteen feet to six feet in depth completely around the lake just shoreward of the central depression, and forms a zone averaging thirty feet in width. This zone is composed almost exclusively of *Potamogeton zosteræfolius* Schum., which grows very luxuriantly, forming a dense tangled mat. The only other plant found in this zone is *P. lucens* L.

(b) A zone of *Nuphar*, extending nearly around the lake, occupying the territory between the preceding zone and the water's edge. This forms a zone between thirty and seventy feet in width, whose lakeward side is about six feet below the surface of the water, while the shoreward side is limited by the

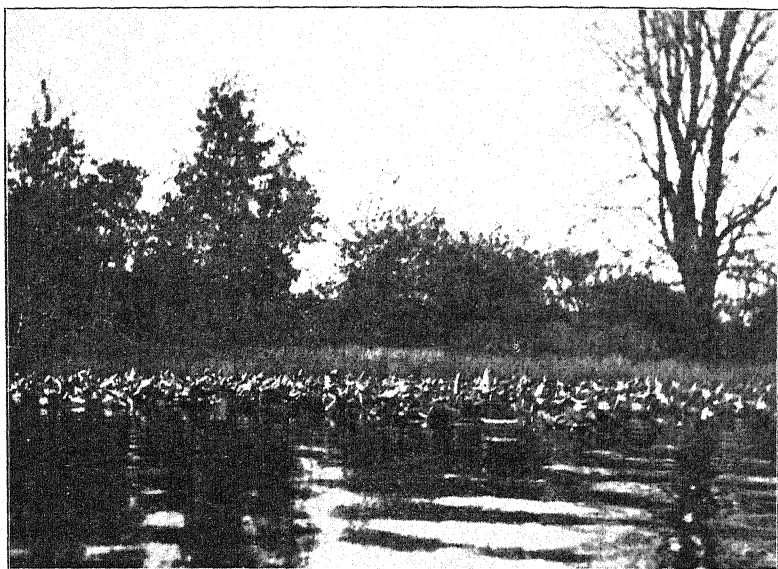


FIG. 2.—North shore of the lake; *Nuphar*, *Carex*, and *Salix* zones; the shrubs in the background are mostly *Populus tremuloides*.

water's edge. The most abundant and characteristic plant in this zone is *Nuphar advena* Ait. f. Its rapid growth and hardiness make it a successful competitor in the struggle among aquatic plants, and it is admirably adapted to the requirements of an advancing plant society, growing as vigorously in water six feet deep as in water six inches deep (fig. 4). Associated with it are *Potamogeton natans* L., *P. lucens* L., *Chara coronata* Ziz., *Dulichium spathaceum* Pers., and *Typha latifolia* L.

In places where for any reason *Nuphar* does not grow or grows only sparingly, *Potamogeton zosteræfolius* comes in; where *Nuphar* grows well *Potamogeton* is not found.

(c) A zone of *Carex* and *Sphagnum*, whose surface is practically at water level, extends landward from the water's edge from six to twenty-five feet. This is an exceedingly well defined zone (fig. 2), and lying so close to the water level it is necessarily saturated with water, and the tough mat of sedges is in many places little better than a floating morass. The soil underlying it is composed entirely of black muck and decaying vegetable matter. The most abundant plants are *Carex filiformis* L., *Sphagnum*, and *Potentilla palustris* Scop.

(d) A zone of *Salix* and *Populus*, varying from ten to forty feet wide, extends entirely around the lake and stands from three to twenty-four inches above the preceding zone. The soil of this zone is almost entirely of vegetable origin; in different parts and at different seasons it contains varying amounts of water. It never becomes mesophytic in character, and is often hydrophytic. A very few vigorous mesophytic species occur with the characteristic plants of this zone, but they usually show changes of habit to correspond to their environment. The characteristic plants of this zone are *Salix alba* L., var. *vitellina* Koch, *S. lucida* Muhl., *S. myrtilloides* L., *Populus tremuloides* Michx., and *Ulmus americana* L.

(e) A zone of *Gramineae* and *Compositae* lies just outside the last zone, and is from six to thirty inches above it. In this zone there are adaptations to past, rather than to present conditions. It is the transition zone in which mesophytic species begin to mix with hydrophytes, its landward border merges gradually into the vegetation of the surrounding country. The greatest admixture of terrestrial plants occurs on the north and southeast shores, where the struggle between plants has been most severe for some time. While it is difficult to designate distinctly characteristic plants for this zone, the following are among the most constantly recurring species: *Spiraea salicifolia* L., *Monarda fistulosa* L., *Rumex obtusifolius* L., *Eupatorium perfoliatum* L., *Salix discolor* Muhl., *Juncus canadensis* J. Gray, *Epilobium coloratum* Muhl., *Hypericum canadense* L., *Nepeta cataria* L., *Sambucus canadensis* L., *Acer rubrum* L., *Gentiana Andrewsii* Griseb., *Bidens bipinnata* L.

Careful collections were made during the entire growing season, and included practically all the species occurring at the lake. They represent forty-three families; 5 per cent. of them are natives of arctic regions; 65 per cent. are natives of North America.

3. INTERZONAL RELATIONS.—A study of the different zones and their relations to one another shows that their positions are not permanent, but that they are slowly encroaching upon the lake, and as a result are filling it with the soil they produce. Each society of plants is a more or less active soil-forming agency, and accordingly as the vegetation progressively changes the advancing zones leave a different soil from the one they found. The vigorous growth of *Potamogeton zosteræfolius* adds by its death and decay a very small amount of humus to the fine clay soil upon which it grows. Nuphar is a much more active soil-forming agent; its strong leaves and petioles projecting above the surface of the water (*fig. 2*) catch and hold most of the twigs, plants, and leaves which are blown into the margin of the lake, until they become water-soaked and sink. The débris resulting from the decay of the water lilies, added to that which they have captured, all goes to building up the bottom of the lake. On account of the limitation of Chara to the Nuphar zone, and the consequent absence of any extensive beds, it is not an active soil-forming agent by the production of marl, as it is in some of the glacial lakes of Michigan.⁵

In the intense competition among the plants of this crowded zone there is a constant tendency to move out in the direction of least resistance. Limited as it is on the landward side by less favorable conditions, the zone must make its advance, if it makes any, into deeper water, *i. e.*, into the *Potamogeton* zone, which it appears to do just in so far as Nuphar is able to adapt itself to the greater depth of water, or as the *Potamogeton* builds up the bottom. At the other side of this zone there is a tension line between the water lilies and the sedges. Whenever in any place the bottom is not more than three or four inches below the sur-

⁵ DAVIS C. A., Jour. Geol. 8: 485 and 498.

face of the water, the sedges begin to move out and occupy the territory thus prepared for them. Perhaps at first they send out a few skirmishers that occupy the top of some muskrat's mound, but generally they advance with an unbroken line and cover the soft muck with a tough quaking mat of vegetation. No advance

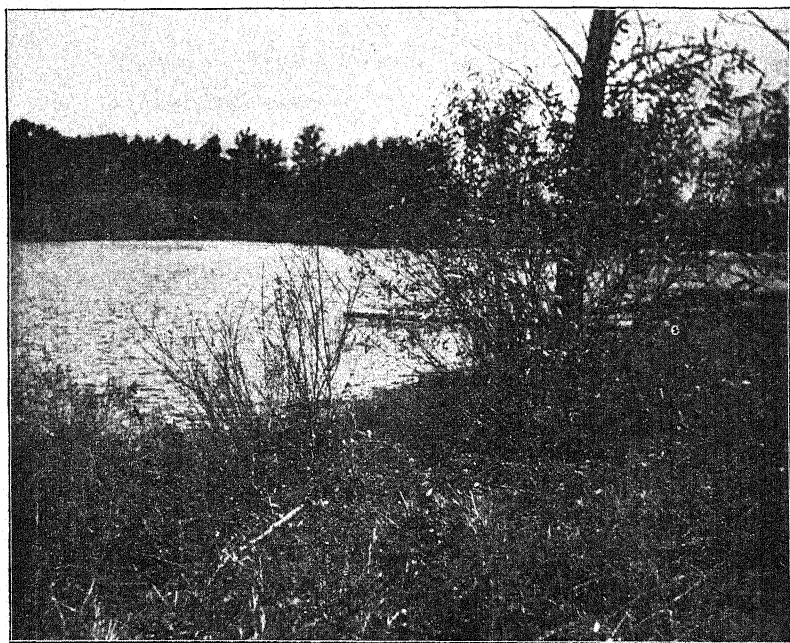


FIG. 3.—Gravelly shore at southeastern corner of the lake; absence of Nuphar and Carices results in a permanent shore-line.

of any extent is ever made without a fairly firm soil to grow upon. *Scirpus lacustris* is one of the foremost plants in the advance. As the *Carex* zone crowds upon the Nuphar zone, so in turn it is itself crowded upon by the *Salix* zone. *Salix rostrata* and *Betula pumila* are among the foremost of the plants encroaching upon the Carices. On gravelly banks and in localities where conditions are unfavorable for the growth of Nuphar, this process of filling does not occur, because the preliminary process of filling by decay cannot take place. The result is that the shore

line in such places is quite well marked and permanent (*fig. 3*).

A few rods south of the lake is the site of the "dead lake" mentioned above, a description of which may, as suggested, throw some light upon the life history of the present lake. At present the only indication of the former pond is an elliptical depression surrounded by representatives of the Gramineae and Compositae zone, but in the spring of the year the depression is filled with water to a depth of about two feet, in which several species of *Polygonum* grow vigorously. Before July the water has all disappeared from this basin and for the remainder of the year it is dry. In the center of the depression there is a group of sedges and ferns which is surrounded by a wide belt of willows; outside of these again is a zone of grass and terrestrial plants. The whole state of affairs suggests that this has been the site of a pond which has been steadily encroached upon by the zones of vegetation in the manner previously described, until now the pond is practically obliterated. The sedges have exterminated the water plants and now the willows have all but exterminated the sedges.

This pond, originating from the primitive lake, must have been essentially the same in character as the lake under consideration; it seems reasonable therefore to conclude that the pond represents an advanced stage yet to be realized in the life history of the lake.

IV. ECOLOGICAL FACTORS.

The plant societies afford unmistakable evidence of the influence of the glacial epochs. The flora of glacial lakes may be compared to boreal islands composed of plants forced southward by the advance of the ice sheet. The sphagnums and sedges flourish best in those conditions which best reproduce boreal environment, and so long as any plant society remains which is distinctly lacustral it will undoubtedly show traces of its boreal origin.

Agencies now at work may be considered under four groups of factors, viz.: hydrodynamic, edaphic, atmospheric, and biotic.⁶

⁶WHITFORD, H. N., BOT. GAZ. 31: 291. 1901.

(a) *Hydrodynamic factors*, referable to the action or presence of water. Small waves are created in the lake by high winds which would eat away the light soil composing the shores but for the fact that such shores are everywhere protected from wave action by a border of water lilies (*fig. 2*). Even in winter this action is prevented because the dead leaves remain *in situ* until the next year. The current of the brook entering from the southeast sweeps away or covers with gravel the accumulations of detritus at that point; as a result, Nuphar and its associates are not found there (*fig. 3*). Aside from this local influence hydrodynamic factors at the present time are so limited in their action that they may be disregarded.

(b) *Edaphic factors*, depending upon the nature of the soil. The humus in the soil formed by the decayed vegetable substances renders it very favorable for plants of the Nuphar, Typha, and Carex types. The presence of water saturated with organic matter in solution plainly influences the character of the vegetation. If Schimper's view⁷ of the effect of humic acid be correct, the explanation of the xerophytic character of some of these swamp plants is that the soil is practically undrained and water with which it is saturated is rich in organic acids.

A microscopic examination of the soil from the deep basin of the lake shows that it is almost entirely composed of finely comminuted, bluish-gray clay with a very few particles of organic débris. The soil from the Nuphar zone is largely composed of fragments of epidermal tissue, moss-stems, diatom shells, bast fibers, grains of sand, and crystals of calcium carbonate from Chara. Chemical analysis shows that nitrates and nitrites are not present in the soil, while phosphates are more abundant.

That portion of the lake bottom which is covered with soil of a calcareous or arenaceous nature does not seem favorable to the growth of the characteristic plants of the lake; the only ones which grow upon such soil are *Potamogeton zosteræfolius* and a few blue-green algae. Evidently lime-containing soils are as

⁷SCHIMPER, A. F. W., Pflanzengeographie, p. 18.

unfavorable for some other swamp plants as they are for sphagnum.⁸

The plants might be classified as to edaphic relations in the following manner: *argillaceous soil*, unattached microscopic plants, diatoms, etc.;⁹ *calcareous and arenaceous soils*, Potamogeton

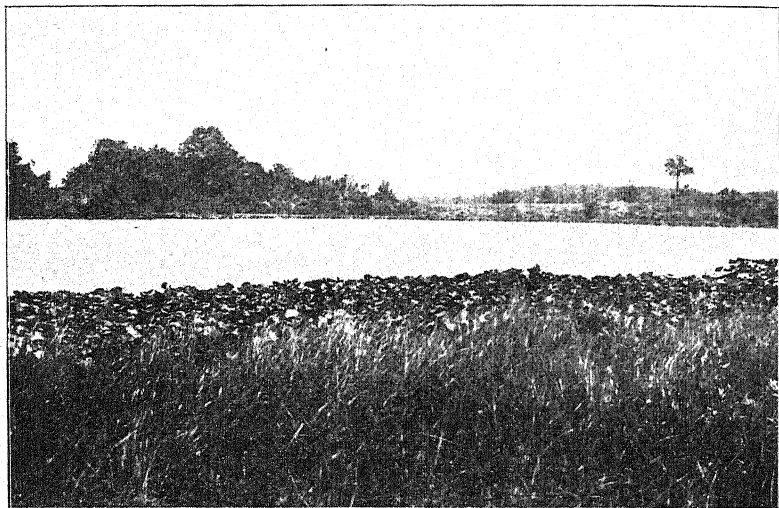


FIG. 4.—Carex and Nuphar zones, showing the massing of these plants; July 1.

zosteraefolius, Blue-green algae (rare), Scirpus lacustris, Potamogeton natans, Chara coronata, Equisetum, Panicum Crus-galli; *carbonaceous soils*, Nuphar, Typha, and Carex societies, Salices, Sphagnum, Populus.

(c) *Atmospheric factors*.—The most important of these is light, because, as I believe, it is this which, aside from food supply, chiefly governs the encroachment of one zone upon another. A moment's consideration will show that the plants struggling for light will have better illumination on the side of the center of the lake than on the side toward the land. Take, for example, the Carex zone (fig. 4). The young Carex and Sphagnum

⁸GANONG, W. F., Trans. Roy. Soc. Canada, 3: 131. 1897.

⁹Under better conditions of light, Chara and Potamogeton would doubtless occur.

plants on the landward side of the zone are overshadowed by the taller *Salix* and *Betula* plants, while on the other side there is almost nothing to diminish the supply of light. In general the plants of a zone which is successful in displacing another zone have a greater capacity for the absorption of light than those plants which they displace. One of the chief advantages of *Nuphar* over *Potamogeton* is to be found in the fact that it sends its leaves up to the surface of the water where they receive the full intensity of the light instead of the diminished amount which is able to penetrate the cloudy water to the submerged species. The lack of light caused by the cloudiness of the water seems to be the only reason for the absence of vegetation from the central deep portion of the lake.

The amount of heat which the different aquatic plants receive also varies with their distance from the surface of the water; however, they seem perfectly able to adapt themselves to these differences.

(*d*) *Biotic factors*.—Fully as important as any of the foregoing factors are the conditions imposed upon plants by the presence of other plants or animals; conditions to which they must adapt themselves if they survive. The competition between different societies of plants is mainly directed toward obtaining light and food. The former has been briefly considered; there are certain biological characteristics which are favorable for obtaining the other. Perennial plants are the most successful in the interzonal struggle; they are usually adapted to xerophytic conditions by their rhizomes, waxed epidermis, and hairy surfaces. There are also special advantages in their manner of reproduction. The possession of underground root-stocks is one of the best adaptations to enable a plant to hold its own against its competitors; young plants are thus sustained by the parent plant until they are fully capable of maintaining an independent existence, and prompt occupation of a given area is easier. The advantage of the willow lies in the great number of seeds produced and the good means of disseminating them. The advantage of the sedges is in the thick mat of

rhizomes and the dense covering of long grassy leaves; the seeds are heavy and tend to fall on the territory already occupied by the parent plant.

Tension lines are the strongest where the environment is most equally favorable for each of two different societies; *e. g.*, the boundary between the *Nuphar* and *Carex* zones is the scene of a severe struggle because the conditions are almost equally suitable for both societies, but where the *Nuphar* zone borders immediately upon the *Salix* zone the tension line is weak.

The ability to compete successfully seems to depend largely upon the extent to which the plants are massed in solid ranks; such a plant society is generally able to force out other plants from the territory available for occupation. The inherent vigor and hardiness of these plant societies due to their northern origin must also be reckoned in attempting to account for the success with which they compete with other forms.

V. CONCLUSIONS.

The work as presented in the foregoing pages is the result of an attempt to study the actual operations of known ecological factors and leave a record of existing conditions in the life history of a glacial lake and its flora. Little attempt has been made to discover new factors or to modify accepted ideas of ecological principles. Most of the statements made can be verified by actual observation; some must be inferred from present conditions. If carried farther, the work should consist in verifying certain statements either by subsequent observation or by laboratory experiment. The results of my study may be summed up as follows:

1. The comparative scarcity of terrestrial plants is a result of the former exclusively hydrophytic conditions which gave aquatic species an advantage which has since been maintained by all other hydrophil species.

2. There is a striking predominance of northern species, undoubtedly the result of the glacial invasion of recent geological times, and of conditions which tend to reproduce boreal environment.

3. The strength of the tension line between zones is increased by the soil-forming activities, because the soil which each zone produces makes the lake more unfit for it and fit for the succeeding zones.

4. An interaction of organic and inorganic agencies has caused and is now causing an unmistakable advance of plants into the lake, which is gradually being filled by the soil they produce. The more important among these agencies are soil, light, and morphological advantages.

5. The struggle for existence in each zone is less successful on the landward than on the lakeward side of that zone.

6. The plants engaged in this severe struggle show a marked tendency to mass themselves in solid ranks.

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BRIEFER ARTICLES.

THE TRICHOME STRUCTURES OF ERODIUM CICUTARIUM.

(WITH FOURTEEN FIGURES)

THE results of observations made by the present writer on the trichomes of *Erodium* are so different from those recently published in this journal¹ that it has seemed worth while to present them in some detail. About four more or less distinct forms of trichomes were found, some of these are glandular, others non-glandular.

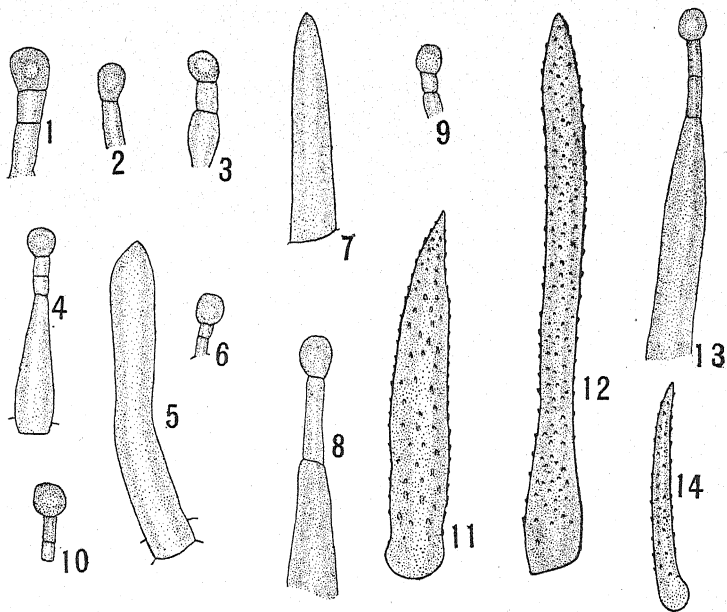
The trichomes of the hypocotyl are chiefly two to three-celled short filaments tipped with a bulbous glandular cell (*figs. 1, 2, 3*). Those of the cotyledon are various; thus the petiole bears some very short glandular hairs (*fig. 6*) smaller than those of the hypocotyl, also a kind with a long somewhat tapering basal cell (*fig. 4*). In addition to these glandular hairs there are some large unicellular hairs (*figs. 5, 7*) scattered here and there among the others. The blade of the cotyledon has in the basal sinus some of these same simple hairs. On other parts of the blade the hairs are glandular. Most of them are short (*fig. 9*), but there are also some longer ones (*fig. 8*) similar to some of those on the petiole (*fig. 4*).

The ordinary foliage leaves are somewhat different from the cotyledons in the trichomes they bear. The petioles have a great number of small glandular hairs (*fig. 10*), and in some specimens not a few longer hairs (*fig. 13*). Often these longer ones consist of five or six cells. In every case the proximal cell is far larger than the others. A thick-walled, rough tuberculate trichome (*fig. 11*) is also present. The leaves are pinnately divided and, as would be expected, the rachis has about the same trichome structures as the petiole. The long tuberculate form (*fig. 12*), however, is somewhat more common than the others, and is here longer than on the petiole. Sometimes these tuberculate structures are two-celled, but this is not a common occurrence. Scattered glandular hairs are also present like those seen on other parts (*figs. 8, 10*). The leaf blades bear many short tuberculate hairs. These are of different sizes. *Fig. 14* shows the most usual size and

¹ PRESTON, CARLETON E., Two instructive seedlings. BOT. GAZ. 33:150. 1902.

form, but some are like *figs. 11* and *12*. They are placed chiefly on the margin of the leaf blade and along the course of the vascular bundles. With them are many short, glandular hairs like those of the petiole (*fig. 10*).

It may be noted that Solereder² notes the presence of the glandular hairs which are here described and figured. He states that in *Ero-*



Trichomes of *Erodium cicutarium*: 1, 2, 3, from the hypocotyl; 4, 5, 6, 7, from the stalk of the cotyledon; 8, 9, from the blade of the cotyledon; 10, 11, from the leaf petiole; 12, from the rachis; 13, from the leaf petiole; 14, from the leaf blade; all $\times 170$.

dium, Geranium, and Pelargonium the cells of the stalk may be all alike or the basal one may be swollen to form a pedestal-like structure (*cf. figs. 9* and *10* with *8* and *13*).

Careful search was made both on the early and later leaves for trichomes with the form of *figs. 4, 8, and 13*, but with the basal cell thick-walled tuberculate. None were found on the material studied, although reported in the paper previously cited. Beside this difference in my own and Mr. Preston's results there are many others. He states

² SOLEREDER, Syst. Anat. d. Dicotyledonen. p. 193. 1899.

that the only modified epidermal structure of the cotyledon is the multicellular glandular hair (represented by my *fig. 8*), while I found all those shown in my *figs. 4-9*. He did not examine the hypocotyl.

By consideration of his results Mr. Preston builds up a theory of the phylogeny of these trichome structures which at once falls to the ground in view of the results reached by me. It seems scarcely worth while to propound theories of phylogeny based on a few observations on a single species. I think also that the theory of the above named writer to account for the lobing of the cotyledons is of no great value. He suggests that the lobing of the foliage leaf is "thrown back" upon the cotyledon. This assumes firstly that "throwing back" can actually occur, while as a matter of fact it yet remains to be proven; and secondly that the cotyledons are homologous with leaves, something which also remains unproven. The suggestion³ concerning the morphology of the cotyledon made at the recent Chicago meeting of botanists of the central states seems more reasonable than the one which would consider the cotyledon as really a leaf.—FRANCIS RAMALEY, *University of Colorado*.

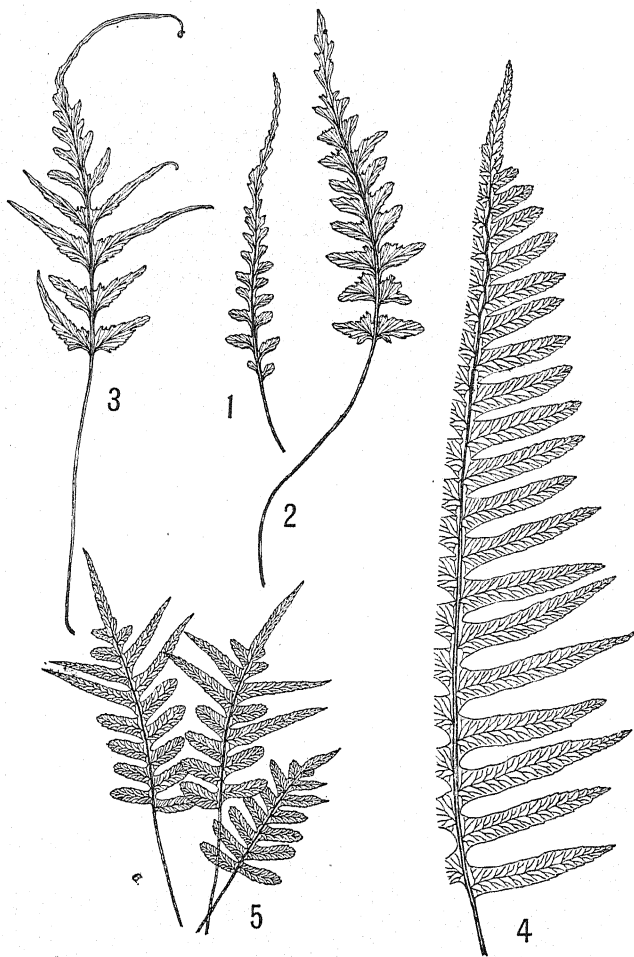
TWO FERN MONSTROSITIES.

(WITH FIVE FIGURES)

DURING the summer of 1900 two remarkable fern monstrosities were found on the Laurel ridge, in northern West Virginia. *Asplenium pinatifidum* Nutt. was found on a spot on the north side of the rocky cañon of Decker's creek, at an altitude of about 1400 feet. There were not a dozen plants, all told, and none of them were quite normal. The species is abundant and typical four miles to the north, across the Cheat. The three accompanying figures illustrate the variability of the Decker's creek material, and will describe the fronds better than words can do. Individual fronds on most, but not on all, of the plants were typical, and insure the determination. Fruiting fronds had normal sori. There were no rooting tips. The region is rather rich in ferns, but I could not find *Camptosorus* in the immediate neighborhood. The "*Asplenium ebenoides*" described by C. E. Waters in *Fern Bulletin* of January 1902, with three different fronds on one plant, is remarkably like this monstrosity.

³ LYON, HAROLD L., The phylogeny of the cotyledon. To be published in *Postelsia*, Annual of the Minnesota Seaside Station, season of 1891.

Polypodium vulgare L. was found in one of the formations known locally as "rock cities," flat hilltops of sandstone, broken so as to leave



FIGS. 1-3. *Asplenium pinnatifidum*.

FIGS. 4-5. *Polypodium vulgare acuminatum*.

parallel "streets" twenty or thirty feet deep and not so wide at an elevation of about 2000 feet. Typical plants were abundant. But in one small patch, hardly more than ten feet square and covering one free rock, there was a marked tendency toward pointed tips of the

frond segments. On young fronds especially the segments near the apex were often more than twice their normal length, and acuminate. On older fronds the modification was less excessive, and occurred as frequently on basal segments. This looks like as distinct a freak as var. *cristatum* or var. *cornutum*, or any of the monstrosities listed with names in Rabenhorst's *Kryptogamen-Flora*. If a name for it is worth while, it might be called monstr. *acuminatum*.

While they are not necessarily any support for De Vries' views on the origin of new plant forms, the value of such freaks as these in the study of the questions De Vries has brought prominently to the fore is self-assertive.—EDWIN BINGHAM COPELAND, *The University of Chicago*.

CURRENT LITERATURE.

BOOK REVIEWS.

Goebel's *Organography*.

THE FIRST PART of the second volume of this great work on the organography of plants has already been reviewed in this journal.¹ The second and concluding part,² now before us, deals almost exclusively with reproduction in pteridophytes and seed plants. The principal subjects are (1) the function of the shoot in reproduction, under which are included the flowers and sporophylls of pteridophytes, gymnosperms, and angiosperms; and (2) the reproductive organs, the principal headings being the mature sporangia of pteridophytes, development of sporangia, hypothetical phylogeny of the formation of sporangia, apospory, microsporangia of seed plants, megasporangia of seed plants.

The work, in large part, is based upon the author's own observations, and many facts in the development of pteridophytes and spermatophytes, as well as the theories drawn from them, are published here for the first time. As might be anticipated from the writer's previous work, the biological side of the subject is strongly emphasized. It is interesting to note that the term "flower," while not made sufficiently elastic to include the sporangial region of *Onoclea*, is nevertheless extended beyond the spermatophytes and applied to the strobili of *Equisetum*, *Selaginella*, etc. According to the author, a flower is "a shoot beset with sporophylls," but how far the boundary is to be pushed is a subjective matter. Bisporangiate flowers are regarded as primitive, most monosporangiate flowers being due to suppression. Bower's classification of the ferns into *Simplices*, *Gradatae*, and *Mixtae* is regarded as useful.

It is very unfortunate that the book contains no index. The table of contents is rather full, but cannot supply the place of an index when one wishes to find some particular thing without a provoking delay. The references to literature are meager and indefinite, and are to be found only as footnotes. The book is essential to the morphologist and ecologist, and it is to be hoped that the English translation will not be long delayed.—CHARLES J. CHAMBERLAIN.

¹ BOTANICAL GAZETTE 31: 204. 1901.

² GOEBEL, K., *Organographie der Pflanzen insbesondere der Archegoniaten und Samenpflanzen*. Zweiter Teil. Spezielle Organographie. 2 Heft: Pteridophyten und Samenpflanzen. Zweiter Teil. 8vo. pp. 649-828. 107 illustrations. Jena: Gustav Fischer, 1901. *M* 5.

MINOR NOTICES.

DR. ROLAND THAXTER,³ in continuing his studies of Laboulbeniaceae, has described numerous new species, adding no fewer than forty to the genus *Laboulbenia*, and describing as new genera *Herpomyces* (9 spp.), *Acallomyces*, *Ecteinomyces*, and *Coreomyces* — J. M. C.

THE NINTH PART of Wiesner's *Die Rohstoffe des Pflanzenreiches*⁴ concludes the nineteenth section on *Unterirdische Pflanzentheile* (to p. 571), contains the twentieth part on *Blätter und Kräuter* (pp. 572–625), and begins the twenty-first part on *Blüthen und Blüthentheile*. — J. M. C.

MISS ALICE EASTWOOD has published a *Flora of the South fork of King's river*, being no. 27 of the publications of the Sierra club. This is the first attempt to prepare a manual of the flora of the southern Sierra Nevada; and the purpose of this preliminary publication is both to record the plants of an interesting region and to provide a simple guide for those not specially trained. — J. M. C.

PARTS 213 and 214 of Engler and Prantl's *Natürlichen Pflanzenfamilien* have appeared.⁵ The former contains the conclusion of the Isoetaceae by R. Sadebeck, and Cycadofilices, Cladoxyleae, Lyginopterideae, Medulloseae, Cycadoxyleae, Protopyteae, and Araucarioxyla by H. Potonié; also a supplement on Marattiaceae and Ophioglossaceae by von Bitter. The latter part contains a continuation of the Pottiaceae by V. F. Brotherus. — J. M. C.

Y. YABE⁶ has published a revision of the Umbelliferae of Japan, the prefatory notes being in English, and the body of the paper in Japanese. The revision includes 40 genera and 95 species, 28 being endemic, and 12 introduced. The largest genus is *Angelica*, in which several new species are described. The author appears not to have had access to the recent *Monograph* by Coulter and Rose, all reference to their work being in connection with the much earlier *Revision*. — J. M. C.

PERCY LEROY RICKER has published "A preliminary list of Maine fungi," being no. 3 of *The University of Maine Studies*. A "historical sketch of the study of the Maine flora" is given, followed by a "list of works and papers treating of Maine fungi." So far as possible, the collection containing the specimen cited is named, so that the right of any species to be

³ Preliminary diagnosis of new species of Laboulbeniaceae. V. Proc. Amer. Acad. 38: 9–57. 1902.

⁴ WIESNER, JULIUS, *Die Rohstoffe des Pflanzenreiches*, etc. Volume II, pp. 481–640. figs. 156–199. Leipzig: Wilhelm Engelmann, 1902. M 5.

⁵ Press of Wilhelm Engelmann, Leipzig.

⁶ *Revisio Umbelliferarum Japonicarum*. Reprint from Jour. Coll. Sci. Imp. Univ. Tokyo. 16²: [repaged] 1902.

regarded as a member of the flora can be tested. The classification is that of Saccardo's *Sylloge Fungorum*. The list includes 370 genera and 1136 species.—J. M. C.

PROFESSOR AVEN NELSON⁷ has prepared a *Key* to the common flowering plants of the Rocky mountain region, to be used by elementary classes of secondary schools in their first contact with the local flora. Such keys are insisted upon by publishers, much to the discomfort of botanists. But if they are to be published at all, they should be prepared by some one familiar with the flora. For the region presented in the *Key* before us no better selection could have been made than Professor Nelson, and every page shows familiar field contact. A few hundred plants of the spring and early summer are selected from the thousands belonging to the flora, and their descriptions and the keys are admirably simple and direct. Of course the author hopes that the little book will serve in inducing the proper study of the flora through the regular manuals.—J. M. C.

C. H. OSTENFELD,⁸ Inspector of the Botanical Museum of the University of Copenhagen, has undertaken to edit an illustrated arctic flora, published in English, the first part of which has just appeared. At the suggestion of Professor Warming, it was begun by the late Mr. O. Gelert, who had associated Mr. C. H. Ostenfeld with him. In March 1899, Mr. Gelert died, but about half of Part I may be credited to him. The ferns and seed plants of the arctic regions are recorded in many scattered lists, each author using his own nomenclature, so that their study is quite troublesome. This *Flora Arctica* includes all regions north of the limit of trees. A prefatory bibliography cites about 95 titles. The pteridophytes are represented by 30 species; the gymnosperms by 3; and the monocotyledons by 179, 54 of them being species of *Carex*. The printing and figures are excellent, the descriptions clear and sufficiently full, and the keys very simple.—J. M. C.

HEALD'S *Elementary Biology*⁹ is a laboratory guide covering a year's work for college students. It is unique in that there is as much space devoted to plants as to animals. Directions for working out a specimen of each of the great plant groups, including Schizophytes, Fungi, and Lichens,

⁷An analytical key to some of the common flowering plants of the Rocky mountain region. pp. vii + 94. New York: D. Appleton & Co. 1902.

⁸*Flora Arctica*, containing descriptions of the flowering plants and ferns found in the arctic regions, with their distribution in these countries. Part I. Pteridophyta. Gymnospermae, and Monocotyledones, by O. GELERT and C. H. OSTENFELD. Published by the Carlsberg fund: Copenhagen. 1902.

⁹HEALD, F. D., Laboratory manual of elementary biology. 8mo. pp. viii + 287. Binghamton (N. Y.): Willard N. Clute & Co. 1902.

are given in minute detail. The forms described were chosen evidently upon the basis of their widespread distribution, rather than because they are typical of the groups they illustrate, or are important from the standpoint of evolution. Spirogyra, Vaucheria, and Chara are the filamentous forms selected to give the student an impression of the green algae, and Marchantia is the only liverwort. It is an open question whether the day for laboratory guides has not passed. The well-trained teacher does not need one—finds it a hindrance in maintaining the plasticity of laboratory work, which should change year after year with the availability of desirable material and the personnel of the class.—F. M. LYON.

A NEW LABORATORY MANUAL of botany has been provided by Dr. Otis W. Caldwell.¹⁰ The book is the result of direct and personal contact with the needs and possibilities of botanical instruction in secondary schools of the middle West. It has avoided the too detailed and technical directions of manuals better adapted to colleges than secondary schools; and at the same time selects the essential features of the subject as now presented in the best schools. It does not seek to eliminate the teacher or the good reference book, but depends upon both to fill out and coordinate. It well meets the demands of schools where time and facilities and the age of pupils forbid the demands often made by zealous but inexperienced university instructors. A good selection of material is presented, so that there may be no difficulty in securing something illustrative. Of course, the wooden teacher will think that everything mentioned is to be used, but for such no suitable book can be written. The first part of the manual suggests ecological and physiological studies; the second part deals with the essentials of morphology.—J. M. C.

THE NINTH PART¹¹ of Engler's *Pflanzenreich* is a book of 437 pages, containing the Myrsinaceae by Carl Mez. After the usual introductory discussion, the 32 genera of this great tropical family are presented. The seven new genera are *Conandrium*, *Sadiria*, *Afrardisia*, *Tetrardisia*, *Amblyanthopsis*, *Discocalyx*, and *Grenacheria*. The total number of species described is 933, of which 348 are new. The large genera are *Ardisia* (235 spp.), *Rapanea* (136 spp.), *Maesa* (102 spp.), and *Embelia* (92 spp.). The fossil forms of nine genera are also described. The vast amount of material to be investigated in a single family like this is an impressive illustration of the magnitude of the work undertaken by Professor Engler and his associates.

¹⁰ A laboratory manual of botany. pp. x+107. New York: D. Appleton & Co. 1902.

¹¹ ENGLER, A., Das Pflanzenreich. Regni vegetabilis conspectus. Heft 9. Myrsinaceae von Carl Mez, pp. 437. Leipzig: Wilhelm Engelmann, 1902. M 23.

The tenth part¹² contains the Tropaeolaceae by Fr. Buchenau, who recognizes 50 species, but describes no new ones. The eleventh part¹³ contains the Marantaceae by K. Schumann, who after a somewhat detailed preliminary discussion presents the 26 genera, 11 of which (*Actoplantes*, *Sarcophrynium*, *Stachyphrynium*, *Halopegia*, *Afrocalathea*, *Monophrynium*, *Ctenophrynium*, *Phacelophrynium*, *Pleioestachya*, *Monophyllanthus*, and *Monotagma*) are described as new. The species number 277, the large genus being *Calathea* with 103 species, and 42 new species are described.—J. M. C.

IN A PAPER on plant distribution Bruncken¹⁴ has contributed some valuable ecological data. The first topic is the succession of forest types in the vicinity of Milwaukee. Three mesophytic associations are discussed; viz., oak, basswood-maple, and elm-ash. The oak is the most prevalent, though evidence is not lacking that it would become replaced by the basswood-maple association if not interfered with by man. Mixed with the basswood and maples near Lake Michigan the beech is found. This, the author states, is probably due to lake climate. There is evidence that a more xerophytic forest of white pine and white birch once prevailed along the lake shore. The second topic is the distribution of the genus *Viola*. After a careful study of the distribution of the various species, the author concludes that the occurrence of the more or less xerophytic species depends on the amount and quality of the humus. The third topic is the upland brushwoods of the Milwaukee region, their typical development being treated in detail. The fourth section is a list of plants collected on the Door co. peninsula, Wisconsin; the fifth discusses the forests and brush lands of northern Waukesha co., Wisconsin; the sixth presents lists of eastern Wisconsin plants from the herbarium of the Milwaukee Public Museum; the seventh is entitled "A tamarack swamp in Waukesha co.;" and the eighth is a list of plants from Sheboygan.—H. N. WHITFORD.

A HANDBOOK of New England trees by Dame and Brooks¹⁵ has been added to the list of popular works in botany. Each tree is discussed under several topics, as the habitat and range, habit, bark, winter buds and leaves, fruiting characters, and the horticultural value. The description of the bark and of the winter buds will facilitate the identification of trees in their winter condition. The distribution of the trees in the different New England

¹² *Ibid.* Tropaeolaceae von Fr. Buchenau, pp. 36. M 1.80.

¹³ *Ibid.* Marantaceae von K. Schumann, pp. 184. M 9.20.

¹⁴ BRUNCKEN, ERNEST, Studies in plant distribution. Bull. Wisconsin Nat. Hist. Surv. 2: 17-28, 137-169. 1902.

¹⁵ DAME, LORIN L., and BROOKS, HENRY, Handbook of New England trees, with ranges throughout the United States and Canada. Boston: Ginn & Company, 1902. \$1.35.

states is given with great care and thoroughness. In the case of trees of infrequent or rare occurrence the authority for each station is given. The accuracy of these citations is made still more prominent by a list of authorities cited and of the trees with reference to which each is quoted. The discussions of the habit of trees also show clearly the result of accurate and painstaking field observations. The book is illustrated from excellent drawings by Mrs. Elizabeth Gleason Bigelow. If this volume is to help the student in the field, as the authors purpose, one would wish that the distinguishing characters of the trees were more fully emphasized. The fact that the New England pines, for example, with one exception, may be readily distinguished by the number of leaves in a sheath is not made prominent. A beginner might read several pages before knowing this simple guide to the pines. A combination of the fruit and leaf characters of the elms, birches, maples, and poplars often furnishes a ready test for the determination of the species. That such facts are emphasized, perhaps with one exception, neither by keys nor by typographic arrangement, will detract from the serviceableness of this pocket-sized volume in actual field work. Throughout the volume the authors use the terms fertile and sterile in referring to staminate and pistillate flowers. Such terms perpetuate a mistaken conception, and they are too antiquated for the present knowledge of plant reproduction. With these two exceptions this volume has a stamp of thoroughness and accuracy not often found in botanical handbooks designed for popular use.—C. D. HOWE.

A FLAX DISEASE of wide distribution and much economic importance has been diagnosed, studied, and traced to its cause by Professor Henry L. Bolley,¹⁶ of the North Dakota Agricultural College; and what is of practical moment an efficient method has been found to check or possibly wholly prevent the disease. Every cultivator knows that only a few successive crops of flax can be grown on a given piece of land with profit. The yield constantly decreases, and no system of manuring or cultivation has been found to overcome the difficulty. An interval of seven to eleven years is required before flax can be grown again with profit upon such a field. The trouble appears to exist alike throughout Europe and America. It is now ascertained to be due to a fungus, introduced chiefly with the seed, which is described as a new species of *Fusarium*, as follows:

FUSARIUM LINI Bolley in Bull. N. D. Agric. Station no. 50. p. 37. Vegetative hyphae light colored, 0.7–3 μ in diameter, septate, branching irregularly, ramifying the tissue of the stem and roots of the host. Spore beds (sporodochia) erumpent, compact, slightly raised, distinct but closely grouped upon the stems, pale cream to flesh-colored. Sporophores rather short and closely branched, or conidia sometimes arising from wart-like or nearly sessile prominences upon a compact stromatic base.

¹⁶ BOLLEY, H. L., Flax wilt and flax-sick soil. Bull. N. D. Exper. Station, no. 50; pp. 27–57. 1901.

Conidia normally four-celled, fusiform, slightly curved or falcate, copiously produced in a bud-like manner from the stroma and from short branches of the sporophores, $27 \times 3 \mu$ to $38 \times 3.5 \mu$. Living in the humus of the soil, able to attack the flax plant, producing the disease known as "flax wilt," and causing the soil condition described as "flax-sick soil."

This fungus attacks the young plants of flax and spreads somewhat slowly to older plants, and has the power to maintain itself for sometime saprophytically. The preventive is to moisten the seed before sowing with a solution of formaldehyde, care being taken to have the seed well cleaned, as no means have been found to disinfect bits of straw and imperfect seed mixed with good seed.

The bulletin is a fine example of deductive and experimental research.—
J. C. ARTHUR.

THE BOTANICAL INSTITUTE of the University of Brussels has begun to publish a collection of its work, of which Vol. V, with papers dated 1900 to 1901, is first to appear.⁷⁷ Vols I-IV, containing papers from 1882 to 1900, are in preparation. The volume at hand has the following attractive contents: G. CLAUTRIAU, Nature et signification des alcaloïdes végétaux, and La digestion dans les urnes de Nepenthes; E. VANDERLINDEN, Recherches microchimiques sur la présence des alcaloïdes et des glycosides dans la famille des Renonculacées, with 2 colored plates; J. MASSART, Le lancement des trichocystes chez *Paramoecium Aurelia*, Sur le protoplasme des Schizophytes with 6 colored plates, and Essai de classification des réflexes non nerveux; L. ERRERA, Sur la myriotonie comme unité dans les mesures osmotiques, and Sur une Bactérie de grandes dimensions: *Spirillum Colossus*; FR. VAN RYSELBERGHE, Influence de la température sur la perméabilité du protoplasme vivant pour l'eau et les substances dissoutes; J. STARKE, De la prétendue existence de solanine dans les graines de Tabac.

In the system proposed by Errera for the measurement of osmotic and gas pressures, the "tonie" is the pressure of 1 dyne on 1 ^{sq. cm} of surface; 10000 of these make the myriotone, which is approximately $\frac{1}{100}$ of an atmosphere. In the equation $p\nu = RT$, if p is expressed in myriotonies, R equals 8.32. The osmotic pressure of 0.1 mol. KNO_3 is computed as ca. 443 myriotonies, considerably higher than the commonly accepted figure. Van Rysselberghe finds that while the temperature has great influence on the rapidity of the movement, water and various other substances (glycerine, urea, caffeine, methylene blue, and ammonium carbonate) can pass slowly through the protoplasm at zero. He holds that the slightest pressure is adequate, if given time, to force water through protoplasm or any other permeable mem-

⁷⁷ Recueil de l'Institut Botanique (Université de Bruxelles) publié par L. Errera. Tome V. Bruxelles. 1902.

brane. Massart, on the protoplasm of the Schizophytes, concludes that the central body, even when it occurs, is not the homologue of a nucleus; nor is the "couche corticale" the homologue of a plastid. He regards the Schizophyceae as derived from the bacteria, but the group as a whole as nowise related to any other organisms. In his last paper, Massart introduces a deluge of new terms sufficient alone to form a supplement to any up-to-date dictionary. The analysis of the subject is clear, and in large part logically carried through; and a clean-cut vocabulary is prerequisite to clean-cut thinking, still more to lucid expression. Codifying such a terminology is an unqualified service to those who use it, as Czapek's forerunner has well proven, but every uninitiate will want to go armed with a "Nomenclator Massartianus" before "geanisopachynosis," "tonesagotic," "cathaptotropic," and the scores more like them become familiar terms.—E. B. COPELAND.

NOTES FOR STUDENTS.

NINE SPECIES of the Corallinae (verae) from Port Renfrew are described and figured by K. Yendo.¹⁸ Three of these are new species, viz., *Cheilosporum MacMillani*, *Corallina vancouveriensis*, and *Corallina aculeata*.—B. M. DAVIS.

THE NEW *Oscillatoria beggiatoides* is a colorless sulphur-bearing organism described by Arzichowsky,¹⁹ and considered by him as a transition between *Oscillatoria* and *Beggiatoa*. The sulphur grains are very small and lie close to the cell wall. The account of this interesting form is to be found among the descriptions of several species of *Beggiatoa*. It deserves better treatment in a language and a journal that will reach more botanists. The paper is written in Russian, with a very short and unsatisfactory résumé in German.—B. M. DAVIS.

PTERYGOPHORA CALIFORNICA is described and figured by MacMillan,²⁰ who presents some interesting observations on its anatomy and development. *Pterygophora* is a surge plant growing below the zone of *Lessonia* and above that of *Nereocystis*. The general morphology is closest to *Alaria*, but the distribution of the sori found in the lateral pinnae, together with the "disposition of cuticular caps in the paraphyses," suggest *Lessonia*. Some of the plants are very large, being ten feet long with stalks three inches in diameter.

¹⁸ YENDO, K., Corallinae verae of Port Renfrew. Minn. Bot. Studies II. 6: 711-722. pls. 51-56. 1902.

¹⁹ ARZICHOWSKY, W., Zur morphologie und systematik der *Beggiatoa* Trev. Bull. Jard. Imp. Bot. 2: 45-46. pl. 1. 1902.

²⁰ MACMILLAN, CONWAY, Observations on *Pterygophora*. Minn. Bot. Studies II. 6: 723-741. pls. 1-62. 1902.

The latter show rings of growth. The young plants have a single blade, as is true of all kelps, the lateral pinnae developing as outgrowths from the stipe below the blade in a manner similar to *Alaria*.—B. M. DAVIS.

HABITUAL POLYEMBRYONY has been observed by Hegelmaier²¹ in *Euphorbia dulcis* Jacq. In about two-thirds of the half ripe seeds there is more than one embryo, the number ranging from two to nine. In the ripe seed the number is smaller, usually two or three, and one of these considerably larger than the others. The embryo which develops from the egg is the only one which has a suspensor, and is also the one which becomes the largest embryo in the ripe seed. Of the other embryos, some come from synergids and some from cells of the nucellus. A large per cent. of the polyembryonic seeds are not capable of germinating on account of the disorganization of the embryo.—CHARLES J. CHAMBERLAIN.

THE TIMOTHY RUST, which has generally been referred to *Puccinia graminis* Pers., was set apart by Eriksson as the result of cultures in 1891-93, under the name *Puccinia Phlei-pratensis* E. & H. In a recent article²² the work of this period is critically examined, and many additional cultures, made during 1894-1900, are reported. The conclusion is reached that the species is autonomous, that it occurs on *Phleum pratense* and *Festuca elatior*, and that it may be transferred sparingly by cultures to *Phleum Michelii*, *Avena sativa*, and *Secale cereale*, but not to *Phleum asperum*, and other grasses. Neither will it infect the barberry, and it appears to have lost the power to form aecidia. It is doubtful if this species occurs in America. It has been reported under the name *P. graminis* once upon *Festuca elatior* (Vermont, 1898), but examination of the original material reveals an error; and once upon *Phleum pratense* (Wisconsin, 1884), which has not been re-examined.—J. C. ARTHUR.

HASSENKAMP²³ describes the development of the cystocarp in two red algae, *Thurella Shousboei* and *Chylocladia kaliformis*, and his results support Oltmanns' theory of the relation which the auxiliary cells bear to the fertilized carpogonium. He finds that when the carpogonium fuses with an auxiliary cell, the respective nuclei remain quite apart, so that the union concerns the cytoplasm alone. The sporogenous nuclei (sporophytic) are then active in developing the fertile portions of the cystocarp with the spores.

²¹ HEGELMAIER, F., Ueber einen neuen Fall von habitueller Polyembryonie. Ber. Deutsch. Bot. Gesells. 19: 488-499. 1901.

²² ERIKSSON, JAKOB, Ist der Timotheengrasrost eine selbständige Rostart oder nicht? Öfv. K. Vet.-Akad. Förh. 1902: 189-198.

²³ HASSENKAMP, A., Ueber die Entwicklung der Cystocarprien bei einigen Florideen. Bot. Zeit. 60: 65-86. pl. 2. figs. 12. 1902.

The results for Chylocladia are especially interesting; since they flatly contradict the conclusions of Hauptfleisch (Flora 75:306. 1892). The latter described a number of secondary cell and nuclear unions following the sexual act and resulting in a large fusion cell. Hassenkamp seems to have overlooked a paper of mine (BOT. GAZ. 21:109. 1896) which showed that Hauptfleisch's results for Champia, a genus closely related to Chylocladia, were incorrect. This omission is the more conspicuous since Oltmanns (Bot. Zeit. 56:128. 1898) tried to smooth over the grave errors of Hauptfleisch by assuming that we were not dealing with the same form. Champia probably presents the same conditions as Chylocladia, as may be judged by comparing my figures with Hassenkamp's.—B. M. DAVIS.

KOHL²⁴ describes an accurate method of measuring the expansion and contraction of pith cylinders, etc., when placed in solutions of different concentrations. The object to be studied is fastened upright by its base in a suitable chamber provided with entrance and exit tubes for the application and changing of plasmolyzing solutions. To the upper end of the object is attached a thread which travels over two small pulleys at the same height and some distance apart. It is sufficiently weighted at its other end to remain taut, and bears a pointer between the pulleys. This pointer traverses a fixed horizontal scale which furnishes a means of measurement.

In the same paper is described a new form of self-registering auxanometer which the author designates as *photographic*. A revolving cylinder, covered with a sensitized collodion film, is enclosed in a dark box, in one of whose sides is a vertical strip of metal provided with an opening of 1^{mm} diameter. This strip is long enough to allow vertical movement without admitting light excepting through the opening. A minute incandescent lamp is fixed to the strip in such a manner that the rays from the lamp traverse the opening at right angles to the strip, and impinge upon the revolving film within the box. By means of a filament passing over a wheel the sliding strip may be fixed to any object whose upward movement is to be studied. As this rises the beam of light moves downward over the film, which, of course, will need to be developed in the usual way to bring out the record.—B. E. LIVINGSTON.

EDWARD C. JEFFREY²⁵ has published a paper entitled "The structure and development of the stem in the Pteridophyta and Gymnosperms." The author reaches the following morphological conclusions: There are two types of cauline central cylinder, protostelic and siphonostelic; the protostelic central cylinder is more primitive, and in its single concentric vascular strand no medulla is present; the siphonostelic central cylinder is tubular,

²⁴ KOHL, F. G., Ein neuer Apparat zur Demonstration von Wachstums und Plasmolyse-Erscheinungen. Ein photographisches Auxanometer. Ber. Deut. Bot. Gesells. 20:208-212. 1902.

²⁵ Phil. Trans. Roy. Soc. London B. 195:119-146. pls. 1-6. 1892.

has a medulla derived from the fundamental tissue, and is characterized by the presence of foliar and ramular lacunae, or by ramular lacunae only; the siphonostelic central cylinder sometimes ceases to be obviously tubular in the adult, and in such cases may be termed adelosiphonic; the siphonostelic central cylinder is primitively concentric, but in the Angiosperms, Gymnosperms, Osmundaceae, etc., has become collateral by reduction; the pith is to be regarded as an inclosed portion of the fundamental tissue. The phylogenetic features of the results are as follows: There are two phylogenetic types of tubular central cylinder, viz., that in which only ramular gaps are present, and that in which both ramular and foliar gaps occur, the former termed cladosiphonic, and the latter phyllosiphonic; the use of these constant and characteristic anatomical features results in the division of the Vasculares into two great primitive stocks—the Lycopsidea, which are cladosiphonic and palingenetically microphyllous, and the Pteropsida, which are phyllosiphonic and palingenetically megaphyllous; the former including the Lycopodiales and the Equisetales, the latter the Filicales, Gymnosperms, and Angiosperms.—J. M. C.

ITEMS OF TAXONOMIC INTEREST are as follows: ALICE EASTWOOD (Proc. Calif. Acad. Sci. III. Bot. 2: 285-293. 1902) has described new species of *Streptanthus*, *Polygonum*, *Eriogonum*, *Garrya*, *Convolvulus*, *Castilleja* (3), *Mimulus*, *Phacelia*, *Gilia*, *Cryptanthus*, *Aster*, and *Madia*, all from the Sierra Nevada mountains of California.—W. A. KELLERMAN (Jour. Mycol. 8: 50-51. *pl.* 1. 1902) has published a new species of *Rhytisma* on *Ilex*.—J. C. ARTHUR (*idem* 51-56) has published 3 new species of *Puccinia*.—ELLIS and EVERHART (*idem* 62-73) have published 59 new species of fungi from the vicinity of Tuskegee, Alabama.—P. HENNINGS (Hedwigia 41: 104-118. 1902), in his first paper on Putteman's collection of fungi from São Paulo, has described as new genera *Puttemansia* (Pezizaceae), *Pseudomelasma* (Leptostromataceae), and *Tetracrium* (Mucedinaceae); and from the Javanese collection of Zimmermann the same author (*idem* 142) has described a new genus (*Zimmermanniella*) of Dothideaceae.—J. B. S. NORTON (Trans. Acad. Sci. St. Louis 12: 35-41. *pls.* 5-8. 1902) has published new species of *Cyperus*, *Argemone*, and *Brauneria* from the southwestern U. S.—T. MAKINO (Bot. Mag. Tokyo 16: 119. 1902) has published a new genus (*Semiaquilegia*) of Ranunculaceae from Japan, said to be intermediate between *Aquilegia* and *Isopyrum*, and founded on *Isopyrum adoxoides*.—J. MATSUMURA (Jour. Coll. Sci. Tokyo 16: pt. 2. *pls.* 4. 1902), in his revision of the Japanese species of *Alnus*, has described 3 new species.—K. YENDO (*idem* *pls.* 7), in a revision of the "Corallinae verae" of Japan, has described 20 new species.—ELMER D. MERRILL (Rhodora 4: 142-147. 1902), in "Notes on N. Am. grasses," has described new species of *Panicularia*, *Poa*, *Bromus*, and *Elymus*.—J. M. C.

INTERCELLULAR KARYOGAMY is the term applied to that condition in the basidiomycetes by which the nuclei are associated in pairs throughout long periods of vegetative activity, but finally fuse in the basidium or teleutospore at the end of the vegetative phase in the life history. The fusion is believed by a number of investigators to be a sexual act, and the association of the nuclei in pairs for so long a time is considered an extension of the period when the gamete nuclei were really differentiated. There are several accounts of the fusion of nuclei in the basidium, several botanists claiming that only two nuclei enter this structure and fuse, while others (Wager and Rosen) have reported as many as three, four, six, and eight concerned with this phenomenon. Ruhland²⁶ in a recent paper throws the weight of his studies upon several of the hymenomycetes in favor of the predominance and possible universality of two primary nuclei entering the basidium and there uniting to form the secondary basidium nucleus, which later divides just previous to spore formation. His conclusions thus accord with the recent paper of Harper (*BOT. GAZ.* 33 : 1. 1902). We do not yet know when the paired condition of the nuclei arises in the life history of any basidiomycete, and this is a very important period, for events may occur at that time which make these nuclei physiologically gametes. However, it is much to know that these pairs of nuclei lie in a definite path of development which ends with their final fusion in the teleutospore and basidium. The more thoroughly we understand these processes in the basidiomycetes the sharper appears the distinction between them and nuclear fusions in the ascus. The two events have no morphological relation to one another. That in the ascus is certainly not concerned with gamete nuclei, whatever may be its physiological significance.— B. M. DAVIS.

²⁶ RUHLAND, W., Zur Kenntniss der intracellularen Karyogamie bei den Basidiomyceten. *Bot. Zeit.* 59 : 487-206. *pl.* 7. 1901.

NEWS.

THE UNIVERSITY OF VERMONT has received from Dr. W. Seward Webb, one of its trustees, the sum of \$6000 for the purchase of the herbarium of C. G. Pringle.

IN CONNECTION with the Royal Botanical Gardens at Peradeniya an experiment station has recently been established for trying on a large scale new products not yet staples. The purchased estate contains 550 acres.

AT A RECENT MEETING of Congress the serial publication known as "Contributions to the U. S. National Herbarium" was transferred from the Department of Agriculture to the National Museum, with a special appropriation of \$7000. This provides for an editorial assistant and an artist, and will enable the Museum to republish certain numbers which are out of print and in demand.

AT THE PITTSBURG meeting of the Botanical Club of the A. A. A. S., the Committee on Nomenclature made the following report through its chairman, Dr. N. L. Britton: "The committee reports that it has held meetings December 29, 1900, and June 30, 1902, and that through a sub-committee has drawn up the basis for a codification of the rules of nomenclature, including the determination of generic types, as previously authorized. The committee recommends that it be given authority to ask the cooperation of other botanists and zoologists in the further consideration of the subjects referred to it, and through their aid to prepare a list of as many types of North American genera as may be possible for presentation, with its report, at a future meeting."

AT THE PITTSBURG meeting of the Botanical Club of the A. A. A. S., C. L. Shear presided, and F. L. Stevens was appointed secretary-treasurer: The following program was presented: H. L. BOLLEY, An anthracnose of flax attacking the embryo within the seed coats; N. L. BRITTON, Carpellary structure of *Sedum pulchellum*, An undescribed species of *Hydrophyllum*; MEL. T. COOK, Notes on material for class demonstration; O. F. COOK, The sterility of coffee varieties, Facts from the history of the cocoa-palm; ARTHUR HOLLICK, A bud from a buried cypress swamp; A. D. HOPKINS, A blank for phenological notes; F. E. LLOYD, Mutual variation in opposite leaves, Vivipary in *Podocarpus*, A cheap and convenient laboratory aquarium, Museum methods: demonstration of life histories; C. L. POLLARD, The Gray polypod in Washington, D. C.; H. VON SCHRENCK, On the germination

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of *Arceuthobium pusillum*; A. D. SELBY, A destructive disease of ginseng under cultivation caused by *Alternaria* sp., A disease of forced cucumbers apparently allied to the mosaic disease of tobacco, tomato, etc.; J. A. SHAFER, *Marshallia trinervata* (Walt) Porter in Pennsylvania, An interesting *Heuchera*; C. L. SHEAR, Notes on *Sclerodema pteridis*, n. sp.; F. L. STEVENS, Notes on *Sclerospora*, Notes on *Symplocos* and *Salvia*, A new character in *Hexastylis*; C. F. STEWART and H. J. EUSTACE, Frost blister of apple and quince leaves. The following officers were elected for the ensuing year: F. E. LLOYD, *president*; A. F. WOODS, *vice-president*; W. R. MAXON, *secretary-treasurer*.

THE RECENT SESSIONS of the Botanical Society of America in Pittsburg marked an important epoch in the history of that organization, and may be taken to be of great importance to the botanical interests of the entire country. Although in existence but eight years as an organization, the funds in the hands of the treasurer now amount to over \$2,700. By the adoption of a resolution at the Denver meeting in 1901 the society committed itself to the policy of expending \$500 per year in grants in aid of investigations as soon as the state of its finances would permit. The income and funds of the society have shown a gratifying and unexpected increase, and this feature of the policy of the society is to be put in force at once, as indicated by the resolutions given below. It is notable that the grants to be made by the society form an example of perhaps the only series of scientific grants ever offered in America by means of funds contributed by actual workers in the branch of science benefited. The first grants may be made at the coming meeting in Washington, as indicated by the resolutions:

Resolved, That applications in aid of investigations may be made at any time by members or associates in good standing. Such applications should be made to the secretary, accompanied by a detailed statement in regard to the work for which the grant is requested, and shall be referred by the secretary to the council. The council shall report upon all applications at the next meeting subsequent to the date at which they are received. The amount of any grant confirmed by the society may be drawn by the applicant from the treasurer within six months after the meeting at which the grant was made, after a proper receipt has been made therefor.

The recipient of a grant must make a report of the progress or of the completed results of the investigations for which the grant was given at the next annual meeting, and at every succeeding meeting until the work in question is finished. Such report must be made in writing to the council, and may or may not be referred to the society. Any and every paper dealing with the results of investigations carried out by the aid of grants as above shall bear the imprint, "Investigations prosecuted with the aid of a grant from the Botanical Society of America."

Resolved, That at the next meeting of the society a grant or grants in aid of investigation may be made in any amount not to exceed the total sum of five hundred dollars (\$500.00) to members and associates of the society.—D. T. MACDOUGAL, *Secretary of Botanical Society of America*.

THE FOLLOWING PAPERS were read before section G of the A. A. A. S. at the recent Pittsburg meeting: JOHN M. BATES, The finding of *Puccinia phragmitis* (Schum.) Korn. in Nebraska; CHARLES E. BESSEY, An instance of a change in the native flora, Note on the fuel value of cottonwood; CHARLES J. CHAMBERLAIN, The origin of the achromatic figure in Pellia; MEL T. COOK, Comparison of the development of the embryo sac and embryo of *Claytonia Virginica* and *Agrostemma Githago*; JOHN M. COULTER, Special haustorial apparatus in connection with the embryo sac of angiosperms; EDWIN B. COPELAND, The ascent of the transpiration stream, Chemical stimulation and the evolution of carbon dioxid; J. W. T. DUVEL, Conditions influencing the vitality and germination of seeds; H. A. HARDING and F. C. STEWART, A bacterial soft rot of certain cruciferous plants and *Amorphophallus simense*, a preliminary report; GEORGE G. HEDGCOCK, The prevalence of Alternaria in Nebraska and Colorado during the drought of 1901; A. S. HITCHCOCK, Notes on Agrostis; MARSHALL A. HOWE, A note on the vitality of the spores of Marsilea; HENRY KRAEMER, The pith cells of *Phytolacca decandra*; D. T. MACDOUGAL, Soil temperatures and vegetation; J. B. S. NORTON, *Sclerotinia fructigena*; GEORGE J. PEIRCE, Some neglected factors in discussions of heredity; CHARLES L. POLLARD, Features of the flora of Cuba; FRANK W. RANE, Effect of acetylene gas-light on plant growth, plant environment, and plant diseases; HERMANN VON SCHRENK, Notes on diseases of western Coniferae; AUGUST D. SELBY, A disease of potato stems in Ohio due to Rhizoctonia; C. L. SHEAR, *Arachniotus trachyspermus*, a new species of the Gymnoascaceae; F. L. STEVENS, Studies in Phycomycete fertilization, *Sclerospora graminicola* (Sacc.); F. L. STEWART, The absorption of water; a function of the ligule and stipulaceous tissue of the grasses; E. MEAD WILCOX, A review and criticism of the botanical curriculum of some of our colleges and universities, from the student's standpoint. The officers elected for the ensuing year are: F. V. COVILLE, *vice-president*; C. J. CHAMBERLAIN, *secretary*.

THE FOLLOWING PAPERS were read before the Botanical Society of America at the recent Pittsburg meeting: MRS. E. G. BRITTON, Studies on reproduction by gemmae of the prothallus of ferns, The genus *Sematophyllum* (*Raphidostegium*), The North American species of *Trichomanes*; N. L. BRITTON, Studies in *Cyperus* and other *Cyperaceae*; W. A. CANNON, Maturation divisions in the pollen cells of hybrid cottons (by invitation); J. M. COULTER, The relations of the botanical associations of the country, Parthenogenesis in seed plants; H. C. COWLES, Suggestions for ecological cartography, A comparative study of the sand dunes of the ocean and lake shore (illustrated); B. D. HALSTED (address of past president), Two centuries of American botany; A. S. HITCHCOCK, North American species of *Leptochloa*; ARTHUR HOLLIICK, Fossil ferns from the Laramie group of Florence, Colorado,

Recent investigations in the Pleistocene flora of Maryland (carried out under the auspices of the Maryland Geological Survey, and presented by permission of the state geologist), illustrated; J. E. KIRKWOOD, The embryology of the Cucurbitaceae (by invitation); MISS E. M. KUPFER, Anatomy and physiology of *Baccharis genistelloides*; D. T. MACDOUGAL, The relations of light and darkness to growth and development; W. B. MCCALLUM, The stimulus to heterophylly in *Proserpinaca palustris* (by invitation); W. A. MURRILL, The genus *Ganoderma* in North America (by invitation); MISS R. J. RENNERT, Dimorphic structure of the phyllodes of *Oxypholis filiformis* (by invitation); P. A. RYDBERG, A study of *Astragalus*; H. VON SCHRENK, A disease of *Catalpa speciosa*; F. L. STEVENS, Mitosis of the primary nucleus of *Synchytrium decipiens* (by invitation); J. J. THORNBURGH, A green organism found in water tanks and reservoirs in Arizona (by invitation); JOHN TORREY, The cytology of the secreting epithelium of *Zea Mays* (by invitation); R. H. TRUE, Tea fermentation; L. M. UNDERWOOD, The genus *Gymnogramma*, and its treatment by English botanists; MISS V. S. WHITE, The Geasters of the United States (by invitation); A. F. WOODS, Some disorganization products of plant cells; CHARLES ZELEM, The dimensional relations of compound leaves (by invitation). The officers elected for the ensuing year are B. T. GALLOWAY, *president*; F. V. COVILLE, *vice-president*; ARTHUR HOLLICK, *treasurer*; D. T. MACDOUGAL, *secretary*; WILLIAM TRELEASE and L. M. UNDERWOOD, *councillors*.

BOTANICAL GAZETTE

SEPTEMBER, 1902

THE RISE OF THE TRANSPIRATION STREAM: AN
HISTORICAL AND CRITICAL DISCUSSION.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.
XXXVIII.

EDWIN BINGHAM COPELAND.

(WITH ONE FIGURE)

1. "Le phénomène de l'ascension de la sève est resté jusqu' à nos jours sans aucune explication plausible," wrote Dutrochet in 1837. Knight had said the same thing in 1801. During the intervening century there have been a considerable number of explanations, plausible enough to satisfy their authors, and a very few which have commanded a wide but temporary adherence. Every theory proposed has been overthrown by direct experiment, or shown to be in conflict with generally accepted principles of physics.

The work of Dixon and Joly and of Askenasy during the past decade has extended the knowledge already possessed in physics as to the cohesive power of water, and by the application of this knowledge these authors have developed a theory which has since almost monopolized the field. Believing that the true solution was to be found in this direction, I set up an apparatus intended to illustrate its application more strikingly than had been done before. This artificial tree had so much in its behavior in common with real trees that when all was done I was likewise unable to explain it.

Thirty-one pieces of glass tubing, each 3^{mm} in diameter and

about 40^{cm} long, were filled with plaster of Paris. As the plaster began to set they were put in a dish of boiled water. They were then boiled, cooled, and boiled again, boiled hard altogether two hours, and left in the same water over night. Air could be located by reflection between the plaster and the glass, as isolated bubbles, making on an average probably one-fifth to one-fourth of the area; the amount of air remaining in this way varied in different tubes. These tubes were connected with heavy rubber tubing; this was done by filling the rubber connections with fresh plaster paste and immediately forcing this out with the pieces of glass tubing to be connected. A continuous tube of plaster of Paris was thus made 12.4^m in height, reaching up the well surrounded by three flights of stairs in the Hull Botanical Laboratory. Four meters below the top was a T tube full of plaster, whose free arm was closed. The lower end was connected with a U tube full of water and mercury in equilibrium; this represented the root. At the top, above another T tube full of plaster with the free arm closed, was the leaf—a sort of inverted osmometer made by filling a funnel with plaster containing some K_4FeCN_6 , tying over it four sheets of parchment paper soaked in K_4FeCN_6 , sealing a glass wall around this, and filling the cup thus formed with a concentrated solution of $CuSO_4$ and $NaCl$. The surface of liquid exposed was great enough so that in the dry, warm air in the hall evaporation was more rapid than the loss was supplied, so that after the first day there was a slow precipitation, and after several days more water had to be added to forestall drying.

The experiment was started at 3:18 P. M., January 14. I recorded with very numerous measurements the rise of mercury in the closed arm of the U tube, most of which measurements it would be a waste of space to publish. The rise was without break or considerable irregularity. It was:

Until January 14, 4:18 P. M., 3.0 ^{mm}	Until January 17, 3:18 P. M., 128.0 ^{mm}
Until January 15, 3:18 P. M., 64.5	Until January 18, 3:18 P. M., 150.5
Until January 16, 3:18 P. M., 101.5	

To obtain the decrease in tension in this manometer these

figures must of course be doubled, the suction developed during five days being then 301^{mm}.

From the very beginning of the absorption of water from the U tube this was a successful demonstration that a column of water above 10^m high in a porous substance, even in the presence of free air, will not break under its own weight. In addition to this it was very soon evident from the lifting of the mercury that maintaining its continuity did not strain it to near the breaking point. With the removal of water from the tube and the elevation of the mercury at its lower end, the tension of the air in the tube of course diminished and the bubbles expanded. During these five days, however, the expansion was not sufficient to cause any general confluence of the bubbles, even in the upper end of the tube.

At 3:18 P. M., January 18, the leaf was removed and the upper end of the tube closed tightly. The height of the mercury thereafter was:

January 18, 4:18 P. M., 151.5 ^{mm}	January 19, 11:30 A. M., 155.5 ^{mm}
January 18, 9:10 P. M., 155.0	January 19, 3:18 P. M., 157.0

The cause of this rise must be sought in the elasticity of the air in the tube. By virtue of this elasticity the suction of the leaf is—to employ materialization as a figure of speech—stored up, and only gradually transmitted to the root. Expressed in terms used with natural trees, transpiration and absorption are not necessarily parallel. This stored up suction is probably represented purely by the rise of 5^{mm} before January 19, 11:30 A. M. The subsequent more rapid rise I ascribe to the fact that the temperature of the hall fell very decidedly that afternoon. Such an effect of cooling, and the opposite result of warming, appeared at some other times.

That the tube could take up more water if the pressure—one atmosphere *minus* 314^{mm} of mercury—at the bottom were increased was evident; still, I thought it worth demonstrating. To this end mercury was poured into the free arm of the U tube until it stood even in both arms. At the same time the T tube 4^m from the top was opened and connected with a capillary

tube 1^m long full of water, whose lower end was in a mercury bath. This was done at 3.40 P. M., January 19. The height of the mercury was:

At the bottom	4 ^m from the top
January 19, 7:20 P. M., 9.0 ^{mm}	450 ^{mm}
January 20, 9:50 P. M., 28.5	530

The suction at the bottom was then 57^{mm}. At 1 P. M. the connection at 4^m had sprung a leak. It was unfair to compare tubes of such different caliber, so the U tube was replaced by a capillary of the same bore as the other, as nearly as possible, and arranged like it. Starting at 1:15 P. M., January 20, the height of the mercury was:

At the bottom	4 ^m from the top
January 20, 3:45 P. M., 130 ^{mm}	455 ^{mm}
6:25 P. M., 186	494
9:10 P. M., 252	531
January 21, 10:30 A. M., 326	550

On January 23 at 10:30 A. M., bubbles having twice been removed from the connection, the mercury at the bottom reached 428^{mm}.

The experiments continued about two months, during which I took several pages of measurements. At one time I arranged the osmometer so as to record the volume of water it absorbed, and found again that for a limited time it could be withdrawn from the tube very much faster than it was taken up lower down. I tried to determine the difference in the suction at the three openings in the tube when the mercury should be drawn up at each until they were in equilibrium; but this was reached so slowly that if there was no other accident, air always came out of the main tube and interfered. During the whole time that the experiment lasted there was a gradual increase in the air in the tube, and with this a decrease in the difference in tension at different heights.

The experiment ended with closing the T tube connections and setting the root end in a solution of eosin. As the eosin rose slowly in the tube, it was very easy to see that it left air between the plaster and the glass; rather more air than was

there when the apparatus was set up, but still so little that it was in small isolated flat bubbles.

While no experiment with any kind of an artificial tube can have the force of a demonstration as to what occurs in a real tree, the behavior of this apparatus was like that in trees as we know it, not only in the general achievement of the elevation of water to a still undefined height, but also in enough known details to make it most probable that the same fundamental physical principles are operative in both cases. But as already said, an analysis showing the elementary factors by which the water is raised has baffled me, even in my own apparatus.

The motive idea in setting up the apparatus—that the cohesion of the water in the tube must be responsible for any suction exerted more than 10^m below the top—was certainly a mistake. This is shown by the readings of the manometers higher up, and also by the continued rise of the mercury at the bottom, after suction at the top ceased, January 18. Both of these observations indicate that the suction developed in the tube is not as great as one atmosphere; that a difference in pressure of less than one atmosphere between top and bottom will lift water much more than 10^m under the peculiar conditions here present. But how? It might be that when water is drawn from the top of the tube it rarefies the air there, and that the suction so arising is propagated downward as largely as possible by the air, and that the bubbles and as little water as possible separating them are thus put in motion. In this way the suction necessary to lift the water should be only equal to that of a column of water equal to the total height of the indices separating the bubbles. But I did not observe that the bubbles moved, and my doubt as to their doing so is very much strengthened by the final observation that the rise of the eosin solution did not drive all the air before it. The tube did become more full of air in the upper part; but I think this was chiefly due to greater suction there, this causing the air present to occupy more space, and hastening diffusion inward through the rubber connections; and two of the "leaves" used leaked. It may be taken

as a fact that in wood there is no general upward movement of free air. Therefore, if it is believed that the behavior of this tube depends on the movement of the bubbles, the experiment is not appropriate to the problem. I shall show that the cohesion explanation is open to exactly the same objections in nature which disqualify it in this tube. This leaves a true explanation to be sought outside of the cohesion of the water, or the rise of the bubbles; by analogy this is probably true in my experiment.

The missing link in the problem is some play of surface tension. Assuming for the moment that the suction is transmitted largely by the air and that the bubbles are carried upward, there is still present continuous water in the plaster, and the upper end of this column would then be subject to the pull of its own 12^m of water, *plus* the suction at the bottom. Its surface tension—which I would rather call capillarity than cohesion here—might enable it to endure this strain. As a matter of fact, though, the tension of the water in the plaster and that of the air and the water around it at the same height must be practically the same. And since the surface tension opposes the movement of the bubbles, but not that of the water, it is natural that the latter should move when either must.

Any further discussion here would be duplicated in sifting the theories on the ascent of sap in nature. The positive result of our experiment is that the water column being continuous, but air being present, a suction of less than one atmosphere can still operate as a suction more than 12^m lower down.

There is an immense mass of published experimentation on the rise of the transpiration stream, whose results are not doubted. During the last four years I have repeated a large part of it for the sake of first-hand familiarity. I shall not add to the literature by republishing work already unquestioned.

II. Dutrochet, in the work quoted in the introduction, says that two forces cooperate to raise the sap: one of repulsion, osmotic in its nature, in the roots; and one of attraction, which is also osmosis—Dutrochet calls it endosmosis—in the leaves.

The driving force in the ascent of sap is root pressure. Seve-

ral explanations of its mechanism are conceivable. A suggestion by Pfeffer, that an unequal distribution within the cell of its osmotically active matter could cause a stream through the cell, has sometimes been adopted as the best solution. But to maintain this inequality would use as much, or rather more, energy than is required to keep up the osmotic pressure present and to lift the water however far it is forced; and this energy would presumably be a net loss to the plant. Detmer (1877) and C. Kraus regarded root pressure as a function of tissue tensions; but the tensions to be observed do not justify this view; and if they did, the solution would not be ultimate, for how should the tissue tensions arise and be maintained? Under the most advantageous conditions external to the active cells, a rhythmic variation in their permeability would result in a root pressure corresponding to the loss of osmotically active matter. But this would make an exceedingly poor machine, unless, as in the original scheme of this kind, by Godlewski, an unequal distribution of the permeability works with the periodic variation. And unequal permeability of different sides of the cell constitutes a perfectly sufficient explanation without any periodicity.

The greatest pressure must be exerted on the side of the cell where resistance to the passage of the solute is greatest. By virtue of this greater pressure when the cell can contain no more water, water will be taken up there, and given off on the other, more permeable side, with at least as much of the solute as would exert an osmotic pressure equal to that under which the water escapes. Artificial cells illustrating this mechanism have been constructed by Sachs (1882) and myself (1900).¹ In so far as its diffusion out of the tracheae into the cortex is resisted, the matter dissolved in the sap in the tracheae exerts an osmotic pressure against the surrounding cells, and to that extent a root pressure can then be maintained without any subsequent loss of solutes by the living cells. It seems probable to me that this suggestion represents the mechanism of the bleeding

¹ Hofmeister's artificial cell (1858: 11; 1862: 145), sometimes referred to as illustrating this action, had all its membranes alike.

of trees in spring better than does the preceding one. The two are closely related, and it would be difficult to distinguish them by experiment. Both have the source of energy in the concentration of the sap. Either provides for only a limited period of high pressure, while the supply of stored, dissolved, or soluble material in the root is carried away by the sap. In its essential features this explanation of the mechanism of root pressure was offered by Brücke in 1844. He illustrated (pp. 194-6) the proportionality of the concentration of the sap to the pressure observed, and said: "Wir werden in der Folge in einer andern Abhandlung näher betrachten, wie sich die Zellen vermittelt dieser löslichen und aufquellenden Substanzen zuerst strotzend mit Wasser anfüllen, und wie dann, in dem sie immer noch mehr Wasser anziehen, das was sie in ihrer Höhle nicht mehr beherbergen können, mit einem Theile der gelösten Substanzen als Saft in die benachbarten Spiralröhren hineingepresst wird." I cannot find that the treatise promised here ever appeared.

The parallel between pressure and concentration is illustrated again by the well-known use of the sap of birch and maple, trees with high root pressure, as sources of sugar. Clark (1874:188) found a root pressure in a *Betula lenta* seventy feet high sufficient to lift water 84.77 feet, the pressure in a root being higher yet. *Acer saccharinum*, with 3.57 per cent. sugar in its sap, registered a pressure of 31.73 feet of water. Clark also reports a pressure of 49.52 feet—6.5 feet above Hale's figure—by grape, the sap being sweet to the taste. The curve given by Schröder (1865) for the concentration of the sap of birch during the season and Clark's for the pressure are parallel, though the inorganic solute decreases constantly. The same author (Schröder, 1869:280) finds 3.44 per cent. sugar in the sap of *Acer platanoides*. The bleeding sap of walnut contains 4 per cent. sugar (Hartig, 1862:88). In all bleeding trees the concentration of the sap and the pressure are supposed to decrease together. In the herbs also (Ulbricht) the concentration of the sap decreases as bleeding goes on. Almost all publications on the concentration of the sap are in such terms that it is impossible to compute the

osmotic strength with any approach to exactness, but they still indicate that it is far more than sufficient to account for the accompanying pressure. On the other side is a statement by Duchartre (1859) that the water guttated by *Colocasia* is almost like distilled. The analysis was by Berthelot, who found traces of KCl, CaCO_3 , and organic matter. The earlier statement by Schmidt, who does not seem to have evaporated the water, that the guttated fluid is chemically pure water, is discordant with all modern results. Unger (1858) found 0.056 per cent. of solid matter in it. For other literature see Burgerstein (1889:405). To account osmotically for this guttation the water would have to be more concentrated than that absorbed by the roots by perhaps 0.03 per cent. of KCl.

According to Strasburger (1891:851), "Belegzellen" are rich in content during the time of bleeding, but not afterward. Still, Strasburger doubts their passing this content into the tracheae, and so setting up a root pressure; but his reason against this seems to be chiefly *a priori*, and based on the unsound assumption that the cells would be obliged to lose the sap in the same concentration in which they hold it.

In herbs, especially in young seedlings, it is very common to find bleeding or guttation during only a part of each day. The same plants in which guttated drops are found in the morning are likely to contain air under a decidedly diminished pressure in the afternoon. The reason is that the roots cannot furnish water as rapidly as it evaporates. But it is also possible that the activity of the roots is less by day, the removal of the hydrostatic pressure in the tracheae stimulating the active cells to become less permeable to their solutes on that side, and so economize their contents when it would be useless to let it escape. Labillardière, according to various text-books, says the palm *Arenga saccharifera* bleeds a sap richer in sugar by night than by day. The daily periodicity in pressure occurs also in trees. The bleeding of *Carpinus* (Strasburger, 1891:841) begins during the night and ceases before noon. Birches may also cease to bleed before noon (Detmer, 1887), but may con-

tinue until after 2:00 P. M., even on bright days, as I have observed in *B. lenta*. Ernst (1876:35) tells of water guttated by *Calliandra Saman* falling like a fine rain all day.

Root pressure rises rapidly with the temperature of the ground. The bubbles of air in the tracheae enlarge when warm, and, as Sachs points out (1860; Hofmeister, 1862), this will force water upward and may well work with real root pressure in the spring bleeding of grape, maple, etc. I would hesitate to ascribe so much importance to it, however, as does Strasburger (1891:833 *seq.*). If bleeding were very largely due to it the daily periodicity would be reversed, as sometimes occurs, especially near the close of the bleeding season (Hartig, 1863:277; Clark, *l. c.*).

According to Wieler (1893:63) guttation is dependent on the presence of free oxygen. Wieler construes this as an argument that root pressure is caused by differences in concentration maintained within the cell. But Purjewitsch's (1897)² discovery of the great influence of oxygen on diffusion through the protoplasm converts Wieler's point into a better one for the otherwise more plausible theory that root pressure depends on permeability to the solute.

The minor rôle played by root pressure in the ascent of sap is obvious from the limited work possible by any pressure to be observed, and from the fact that it is altogether absent at the times during the season when transpiration is most active. On the latter point enough has been said. As to the pressures, those which I have cited are the highest ever recorded, with the best subjects growing in our climate. With ordinary subjects which show any root pressure at all it is usually only a few centimeters, or only millimeters, of mercury. It is true that the pressure as measured by manometers is an excess over the counter pressure of the atmosphere. Root pressure unable to overcome this can be demonstrated in many plants (Scheit, 1886:701; Wieler, 1893:97 *seq.*) if the atmospheric pressure is

²From instances in which the food normally diffuses from the cell without apparent change, I am unable to agree with Purjewitsch in ascribing the effect of the presence or absence of oxygen to its action on enzymes.

removed; but in living cells, when the gas higher up in the stem is not more dilute than that outside, it must exert a similar resistance of at least an atmosphere to the rising sap. In the spring when root pressure is most active, manometers inserted at different heights show pressures corresponding to columns of water of the same differences in height (Clark; Hofmeister, *Flora*, 1858:4.) So water in the tree, when it practically fills the lumina, will at most be shoved up as far as the same pressure would drive it in a glass tube. As we will see later, this is not necessarily the case when the wood contains a great deal of rarefied air.

III. Let us now turn to the force of attraction. It is a matter of common understanding that the leaves have available practically unlimited energy for the elevation of water if only it can be so applied. Of the radiant energy absorbed by the chlorophyll but a small fraction is used in photosynthesis; and evaporation, by cooling the leaf, enables it to absorb more heat from the air. This energy is nearly all used for evaporation. Whether we say with Mayer (1895:366) that the cause of evaporation is "*die lebendige Kraft der Wassermoleküle durch welche diese geneigt sind Dampfform anzunehmen*," or with Nägeli (1860:38) that the energy is drawn from the tissue itself, it ultimately comes as heat and light from without. Whatever force has been used in drawing water up to the leaves must be overcome when it has evaporated; which slightly decreases the amount evaporated. At the same time, the same force becomes available for the elevation of more water. The energy thus indirectly used in lifting is relatively inconsiderable. In a former note (1900), figuring the latent heat of evaporation, which varies with the temperature, at 536 calories, the mechanical equivalent of a calorie being 424, I pointed out that the energy used in vaporizing water would lift it about 142 miles. At ordinary temperatures the latent heat of vaporization is enough greater to raise this to perhaps 156 miles. Of course, no large part of this could be used in lifting (Rodewald, 1892). Nägeli (1860:39) says that the evaporation uses in general 131

times as much energy as assimilation, which in turn uses eighty times as much as it takes to lift the water; obviously this depends upon how far this is lifted.

It must be almost exclusively true in nature, as Askenasy (1895 : 333) has it in his very clear and concise scheme of the energy changes in the rise of water, that the chief force in the leaf which removes the sap from the tracheae and in spite of which it evaporates, is osmosis. To be complete, it may be said that imbibition intervenes between osmosis and evaporation to get the sap through the wall of the mesophyll cells from which most of it evaporates. On the other side, it also intervenes in the walls between the living contents of the mesophyll and the tracheae from which they draw water. Very likely a little water passes out in the walls from the vessels to the point of evaporation independently of osmosis; at any rate this is not prevented by suberization of the anticlinal walls, as in the endodermis of roots. When water evaporates from a mesophyll cell, the concentration of its sap increases and the tension of its wall is eliminated. In both of these ways, but at first in chief part in the second way, the cell is enabled to draw more water from whence it can, from the tracheae. Mechanically this elimination of the tension of the wall suggests the elasticity of the wall by which Böhm (1864) at first sought to explain suction by leaves; but the actual tension always remains a stretching. In some of his latest work (1890, etc.) the same author denied the play of osmosis on the ground that transpiration is not stopped by death. Evaporation does occur after death, evaporation of the water in the leaves, and of as much more water as can be drawn up before enough air diffuses into the walls and lumina of the tracheae to close them to water; in leaves of firm texture, especially in evergreens, this does not soon occur. But this is not ground for doubting that in living leaves the water passes through the cells, necessarily, by osmosis.

All water passes from the tracheae by imbibition, and so far as the mechanism of movement in the tracheae is concerned, it matters not whether or not osmosis is active in the leaves (Ask-

enasy, 1895; Dixon, 1896; Darwin, in Darwin, etc., 1896: 336-7; Joly, *ibid.* 649). Regarded purely as a transpiring machine, the live leaf is superior to the dead one chiefly because it does not incapacitate itself by drying. Dixon's suggestion (1896, I) is a good one, that dead leaves transpire less than fresh live ones because the collapse of their cells closes the intercellular space. But his other idea, that the fact that flaccid live leaves evaporate only half as much water as dead ones is due to their loss of "turgescence," seems to me to rest on a confusion of the osmotic pressure of the solutes in the cell sap — which I have tried (*Annals of Botany*, June 1902) to distinguish as "turgor" — and the state of "turgescence" caused by the "turgor" when enough water is available. It is by virtue of its "turgor" that the mesophyll absorbs water from the tracheae; and the "turgor" is greater, because when the cell shrinks its sap becomes concentrated, in flaccid than in fresh leaves.

The osmotic pressure in the leaf cells is much more than is used in lifting water. From very numerous tests by plasmolysis I can say that it is in general about equivalent to that of 3.5 per. cent KNO_3 . In some plants it is much higher; for instance, in grasses and in halophytes. In typical spongy parenchyma the turgor cannot be accurately measured. In the bundle sheath it seems usually to be slightly less than in the palisade tissue, but this may be because the tests of the latter is less accurate. It also seems to be on the whole a little higher in trees than in herbs, but this also may be because the cells are usually smaller in trees, making the turgor appear too high. Dixon (1896, II) has undertaken to measure the turgor of leaves by ascertaining the gas pressure sufficient to collapse the cells and force water from them into the tracheae. The method is not a reliable one until we know something about the passage of the gases into solution and their diffusion into the cells. We have no information as to the turgor in the leaves of very high trees, 60 to 150^m in height, but to lift the transpiration stream it need not be higher than that of herbs.

The mesophyll cells supply themselves with water from the

fibrovascular bundles, whose finest ramifications are fine tracheides.

IV. So far, the mechanism of the movement of water is a very simple problem. The difficulty is in the next step, in explaining how suction in the tracheides and vessels of the leaves can be propagated so as to cause an upward movement along the stem, and even from the roots of lofty trees. Summarizing a part of our empirical knowledge may facilitate a subsequent analysis of the theories. The path of the transpiration stream is, speaking for trees, in the younger wood. The number of years' growth of gymnosperms and dicotyledons which share in conducting it is very variable. Beside this radial limit, the stream supplying any particular part of the crown—as a single branch—is also limited tangentially. A well-known experiment by Th. Hartig (1853:313) illustrates this. He bored five holes in a tree, meeting in the axis, and filled the cavities with "holzsaurem Eisen;" the tree was afterward cut forty feet higher up, and the figure of a star, one ray corresponding to each hole found stained. Experiments on the lateral movement of water by overlapping cuts from opposite sides date back to Hale's. As on various other points, the most valuable collection of data is Strasburger's (1891: 595 *seq.*; 1893: 34, 37). Other more notable work on transverse movement is by Darwin and Phillips, Vesque (1883, 1891: 576), Wiesner (1875). A limit to the ease of lateral movement is necessary in order that any store of water can be retained, while other water moves past it from the ground. It is also necessary for the maintenance of any proportion of air and water in the individual channels.

With the exception of a time in spring when the lumen of some trees becomes full of water forced there by root pressure, the tracheae always contain a considerable amount of air. Scheit maintains that the spaces in the lumen not occupied by liquid water are filled with its vapor, and Sachs in his latest work (1892) inclines toward the same view. But before Scheit's time there was abundant proof of the presence of air, including analyses by Böhm (1878), Faivre and Dupré, and others; and more

recently it has been redemonstrated by Schwendener (1886: 563), Tschapoltwitsch, and Strasburger (1891: 677). The air content of the heart is rather fixed, but that of the sap wood decidedly variable. With only the same class of exceptions as to the presence of air at all, the air in the tracheae is under a lower tension than that of the atmosphere outside. This lower tension is one of the reasons for the presence of air in the gaseous form. The water absorbed by roots is saturated with air under the atmospheric pressure and at ground temperature. In the trunk the water is usually warmed and a part of the pressure is removed, both tending to cause the air to come out of solution. It has not been so easy to tell why there is not more air in the wood. But Noll's recent discovery that there is an active osmotic movement of gas between the wood and the air outside throws an altogether new light on this question. At least for vessels in or near the leaves, Noll shows that this osmosis will be very largely outward. Before this discovery, the only known immediate cause of the diminished tension of the tracheal air, aside from the relatively inconsiderable influence of occasional cooling, was the removal of water from the lumina to replace that evaporated from the leaves.

The less air the tracheae contain, the greater will be the change in its tension with a given variation in the amount of water present. Evidently the proportion of water present gives an approximate, though not an exact measure of the tension of the air. This proportion of water is in all cases least in summer, the maximum being in winter in gymnosperms, and in spring in dicotyledons (Th. Hartig, 1868; Geleznow, 1876. R. Hartig, Bot. Zeit. 1883, disputes this). Th. Hartig (*l. c.*, 20) tested the water content of twenty-six kinds of trees, four feet from the ground, before sunrise, and at 2:00 P. M., and found the loss of water varying from 2 to 38 per cent. G. Kraus' most accurate work on this subject comes to the same conclusions, epitomized by Kraus himself in Sachs' *Pflanzenphysiologie*, second edition p. 601, as follows: "Die Pflanzentheile (Stämme, Blätter, Früchte, Knollen, Knospen) . . . sind am Tage kleiner, bei Nacht grösser."

"Diese An- und Abschwellung resultirt aus dem periodisch schwankenden Wassergehalt der Theile; dieser ist regelmässig am Tage geringer, in der Nacht höher." "Der ungleiche Wassergehalt der Organe bei Tag und Nacht ist seinerseits das Resultat aus der ungleichen Thätigkeit der Wasser zu- und abführenden Kräfte." We will return later to the tensions associated with the water content. The rarefaction of the gas in the tracheae is often spoken of as causing a negative tension. The physical condition of a gas makes it impossible that it should exert or even transmit a real negative tension. A gas must always press against whatever confines it; when the gas is rarefied the pressure diminishes, but it can never become a suction.

While lateral movement of water in the wood is difficult, its passage lengthwise of the wood is exceedingly easy. This is easily and conclusively shown by what is known as the "Th. Hartig experiment." As an instructive experiment, we owe this to Sachs; but no one experiment can be identified as "Sachs' experiment," so the misnomer can profitably be retained. As a matter of historical interest it may be remarked that the experiment did not originate with Hartig. Boucherie (1841) had made a technical application of it in substantially the same improved form afterward employed by Sachs. And Biot (*cf.* Biot, 1841) preceded Boucherie, but I have not had access to his earlier papers. Hartig showed that when water was forced out of a stick by warming it, gravity could determine the place of its appearance. Sachs' familiar experiment is to soak a stick in water, dry the ends, place a drop on the upper end, and observe that it is absorbed, while a corresponding drop emerges below. Various woods make good subjects for this experiment, those containing vessels allowing the freest movement. As interpreted by Godlewski (1882:585-7), it shows that the weight of the water held in the wood is sufficient to overcome the resistance to its movement. Schwendener (1886:579; also Strasburger, 1891:773) showed that much less than this pressure is required. Strasburger also showed that an excess pressure of only 20 per cent. is required to cause a movement in sticks of

Acacia as rapid as that of the transpiration stream. Too much air in wood hinders or prevents the movement of water, as proven by Boucherie and many of his successors. It is for this reason that shoots cut in air wilt though the cut end be afterwards placed in water; the lesser tension in the tracheae causing those exposed to fill with air at the outside tension. On the other hand, when the vessels are well supplied with water, the removal of part of it facilitates its movement in response to the "attraction" above—according to Dutrochet. It is my belief that in lofty trees it would be impossible for water to be drawn from the root while the tracheae are even approximately full of it; though of course all that is certain or can be demonstrated empirically is that there is a great deal of space occupied by gas when transpiration is rapid.

In a capillary tube filled with a succession of bubbles of air separated by water (Jamin's chain), the resistance to the movement of the entire column of air and water is very considerable (Jamin, Schwendener, and Steinbrinck). While measurements made in glass tubes are not valid for the tracheae (Strasburger, 1891:815), the movement of the bubbles in the latter is interfered with by the sculpturing of the walls and the remains of the partitions (Kamerling, 1898, I: 978). The result is that a pressure insufficient to move the bubbles will cause a flow of water between the bubbles and the wall.

Vesque (1882; Ann. Sc. Nat. 1883) and Capus observed under the microscope that bubbles did not prevent a current above and below them in the same vessel. Vesque (*cf.* 1891: 384; the original publication was in the *Annales Agronomiques* 11: 1885) afterward determined that this current passed between the bubble and the wall; which was confirmed by Strasburger (1891:703). Pappenheim (1892:161) was unable to demonstrate such a movement; nor could Schwendener, who denied its possibility (1886; 1892:920). I have not found Vesque's experiments exceedingly difficult, either in glass tubes or in tracheae, and will describe some of them briefly later in this paper. The same phenomenon can be conveniently observed in

the rhizoids of the Marchantiaceae. As we are told by Kamerling (1897 : 12), after a bubble is formed in one of the "pegged" rhizoids, it may increase in length downward as well as upward, the water from the lower end flowing past the bubble. Another of Strasburger's experiments (1891 : 819) furnishes as positive proof as that by direct observation; the same experiments which proved that the Jamin's chain was held less firmly in tracheae than in glass showed that a pressure insufficient to move the bubbles would force water through the same tracheae.

V. Some of the theories as to the rise of water, and retaining only an historical interest, may be mentioned very briefly. Knight (1801 : 344) ascribed the ascent of sap to contraction by the medullary rays, "the silver grain," which somewhere touch all the vessels. "Their restless temper, after the tree has ceased to live, inclines me to believe that they are not made to be idle whilst it continues to live." If a tangential surface of wood is exposed during the day, the silver grain appear as minute clefts into which pins may be stuck and be found pinched fast at night. This contraction, he thought, might elevate the water.

Bischoff (1836, Vol. II, pt. 1 : 238, 271) believed the sap to be driven up, not in the vessels but in the cells, by the contractility of the walls, acting under the influence of the living contents. Böhm at one time (1878) held a similar view, omitting, however, as he always did, any dependence on the activity of the protoplasm. He called the movement (p. 230) "*une fonction de l'élasticité des parois cellulaires et de la pression atmosphérique.*" But already in the same paper (p. 236) he recognized that in cells with rigid walls their elasticity is replaced by that of the air in the lumen.

Th. Hartig (1853), observing facetiously that his was the age of steam, thought the cavities of the pits might act as millions of little engines so numerous that when warmed even a very little they could drive the water up.

The agitation of trees by the wind was plausibly used by Spencer to move water in the vessels from the roots, where it was most abundant, to the twigs and leaves where evaporation

created a constant demand; the arrangement being "a sort of rude force-pump worked by the wind."

Scheit suggested that slight differences in temperature might raise the water "auf dem Wege der Destillation" (1885:477). But, as Scheit himself pointed out, this would not raise any mineral food.

VI. While the imbibition theory has had no champion since the death of Sachs, it reigned too long to be passed over in a sentence now. Granting Sachs' claim that the imbibition theory was his personal intellectual product and property, it would seem but fair to confine ourselves in discussing it to the final stage of its evolution. But it was in one of its earlier forms, afterward outgrown by its great exponent, that the theory was dominant. Sachs lists the publications in which this theory was developed in his hands in his *Vorlesungen über Pflanzenphysiologie* (2d edition, 225). Its period of greatest vogue was about the close of the seventies, after the publication of the paper "Ueber die Porosität des Holzes." The imbibition theory said that the water was carried altogether in the walls of the wood elements, where it was absorbed and held by imbibition. The substance of the wood walls was believed to be very remarkable, in "Dass sie (the walls) verhältnissmässig nur wenig Wasser in sich aufnehmen, dass dieses wenige Imbibitionswasser jedoch in ihnen auffallend beweglich ist." The removal of any water from the wood at the top of the tree caused a flow toward the point of loss, the demand for water being thus propagated in the walls to the roots, where it could be satisfied. It had been demonstrated that the forces at play in imbibition far more than sufficed for the elevation of the water; that the water moved easily in wood was certain. That it moved in the walls seemed to have been demonstrated by direct observation of air filling the lumina; by the experiment of Unger (1868), who injected the lumina with wax without preventing the movement of water; and later by Sachs' experiments with sharply bent tendrils, etc.

Sachs elaborated no new theory of imbibition to account for

the movement of water, Naegeli's micellar hypothesis being generally accepted, and accounting satisfactorily for the great force with which the water had to be, and is, held. As I understand the micellar hypothesis, it regards the water as held between the micellae by its surface tension; at any rate, it would say that imbibition and surface tension have a common mechanical explanation. This is not altered in the least by the fact that the presence of the spaces is dependent on that of the water. Since the spaces are indefinitely small, the tension is indefinitely great. In the evaporating surface these spaces become still smaller as they lose water, unless it is immediately replaced from behind, and the menisci formed in them are of such ultra-microscopical minuteness that it is easy to suppose they can draw water higher than any tree reaches. Assuming always that the walls were the path of the water, the imbibition theory was thus complete, and not in open discord with contemporary physical science. As this was not true of any other theory it was but natural that this one was generally accepted, and by a sort of reflex action this strengthened the faith in its premise as to the path.

The identity of imbibition and capillarity was postulated by DeLuc (1791:12), but on evidence—the imbibition of alcohol and ether—which has not been found generally sound. Hofmeister (1862:100) and Unger (1868), who were forerunners in the modern development of the theory, treated them as the same, as did Pfeffer in his unqualified acceptance of this theory in the first edition of his *Physiology*. Naegeli and Schwendener (Mikroskop. second ed. 380) say it is indifferent what the force is called, though formulae based on measurements of tubes of appreciable size need not apply in these invisible interstices. In 1865 (Handbuch, 213) Sachs entertained no doubt that capillarity and imbibition were related. In 1879 (Por. d. H.), however, he regarded the phenomena as distinct, and afterward became most insistent on the difference. This robbed the imbibition theory of its foundation in established physics, and it is very doubtful if it ever could have obtained general credence

in this form. The imbibitionists never offered any physical explanation of the supposed absence of high friction in the fine pores of the wood; this was dismissed as a "natural property" of the wood substance.

The imbibition theory fell with the disproof of its first premise, that the water moved in the walls. Unger's injection experiment was repeated with the opposite result. Elfving (1882:714) plugged the lumina of pieces of wood with cocoa butter and could force no water through them. Scheit (1884) injected sticks with gelatin with the same result. Vesque (1884:188) injected the tracheae of a living branch with cocoa butter and the branch wilted. Errera (1886, I, 31, II) repeated this experiment using gelatin; as did also Strasburger (1891:541). Dixon and Joly (1895) employed gelatin, paraffin, ice, and water vapor to obstruct the lumina, causing wilting in each case. Smith found the movement of water in cucumber stopped or very nearly so by injection with gelatin; the plugging of the spiral vessels by *Bacillus tracheiphilus* caused a gradual wilting, while *Fusarium niveum*, which fills the pitted vessels as well, causes a sudden collapse of watermelon foliage. Vesque (1884), Kohl (1885), and Darwin and Phillips (1885:366) made plants wilt, or checked the absorption as measured by the potometer, by squeezing them until the lumina were presumably closed. The old observation (DeVries) that if a transpiring branch is cut in the air it wilts was recognized as showing that plugging the lumina with air closed the path of the water (Scheit, 1886:172). Against the experiments with bent branches it was pointed out by Russow (1883:99) and Scheit (1884) that bending does not entirely close the lumina. And Dufour's inability to force water through the bends under pressure was ascribed by the opponents of his theory to the entrance of air where his wood was exposed in cutting.

The movement of water in the lumina was directly observed by a number of investigators, notably Vesque. The well-known presence in the lumina of colors and other substances used in detecting the path of the transpiration stream had been ascribed

to the abnormal direct atmospheric pressure against cut surfaces; but without reason, as Van Tieghem (1870:278 *seq.*) found decoctions absorbed by sound seedlings of Leguminosae confined to the lumina of the vessels. Once the imbibition theory was undermined, older objections to it, some of which Böhm had been constantly raising, were granted recognition. It was incontestable that lumina of at least a part of the conducting elements contained water; the imbibition theory could offer no explanation at all of its presence (Böhm, 1878:225; Sachs, 1887:247). The absence of a parallel between transpiration and absorption (McNab, 1874:356; Vesque, 1878) was therefore unintelligible to imbibitionists. The excessive difference in the facility of transverse and longitudinal movement of water was not intelligible on the basis of the distribution of the water of imbibition, the difference in other physical properties of the wood walls being relatively small. The drying out of dead branches of living trees would seem impossible according to the imbibition theory. And there are other minor objections to it which need not be touched upon here.

Our permanent debt to the founders and supporters of the imbibition theory is for placing great emphasis on the easy passage of water through the wood,³ and for suggesting a physical means for this passage. The water cannot escape passing through occasional walls as it rises. And the work of Errera and of Dixon and Joly, already cited, testifies that some water, though far from enough to satisfy the demands of transpiration, can travel in the walls for a considerable distance.

VII. An active rôle in the elevation of the water has been ascribed by many writers to capillarity in the lumina of the elements of the wood.⁴ At the same time it has been recognized

³ Even this is disputed by Janse.

⁴ Recognizing of course that capillarity is not an ultimate source of energy for the rise, but that this is furnished when the water is evaporated. It would indeed be a careless attempt at an explanation which should seek in capillarity the energy to keep a stream moving upward; still, I cannot agree with Kamerling that this would be a "logical error," since the law of the conservation of energy does not itself rest on logic.

that in tubes of such size as these lumina the lifting power of capillarity is not exceedingly great. In a glass tube 10μ in diameter this should be about 3^m . Strasburger (1891:87 *seq.*) found it less in tracheae than in glass, sometimes less than half as much. While the lifting power is determined by the form of the meniscus, it is possible enough that this should be influenced by the nature of the wall. In the absence of direct contrary evidence on the same subject, which is wanting in Schwendener's criticism (1892:912), Strasburger's statement must stand.

The efficacy of capillarity is limited again by the dilution of the air in the tracheae. Naegeli's classical work on capillarity (1866, I, II) showed experimentally that with diminishing atmospheric pressure the lifting power of a meniscus in a glass tube decreases; slowly at first, but rapidly when the pressure approaches zero. The theoretical ground for this is evident from the intimate connection between surface tension and vapor tension. Naegeli found the details to be remarkably dependent upon the temperature. Since the air in the tracheae is always rarefied when transpiration is at all active, and with excessive transpiration the loss of pressure is great enough sometimes to lead to the formation of bubbles of water vapor, the service which capillarity can perform in the elevation of water is most insignificant when the demand for water is most urgent. A repeated, but so far as I can see entirely unwarrantable assumption (Böhm, *Ann. Sci. Nat.* 1878:232; Elfving, 1885:536; R. Hartig, *Bot. Zeit.* 1883; Sanio) has been that each wall across the path of the transpiration stream furnished a fresh starting point for capillarity to work from. There is no reason why a wall should offer any greater resistance to movement of water downward in response to gravity than upward in response to capillarity.

The Jamin's chain has never been shown to have any advantage over a single meniscus in causing a movement of water. For every added meniscus with an upward pull there is one of the same shape whose concavity is downward. The resistance

offered by a long series of bubbles to longitudinal pressure has given the Jamin's chain a place in some theories (Westermaier, 1883; also Hartig, 1882; Vesque, 1884), as an arrangement to hold the water up, forces of a different nature being invoked to elevate it. Statements as to this resistance of the "chain" in glass tubes are very discrepant (Janse, Naegeli, Plateau — as cited by Strasburger, 1891:815 — Zimmerman, 1883); according to the experimental results of Schwendener (1886:569) and Strasburger (1891:819) the resistance to the movement of the chain as a whole is not usually very great in tracheae.

If the pressure against the upper end of such a column of air and of water were diminished or removed, the result would obviously be an elongation of the bubbles, lifting the water supported by them. This would operate most at the top, and would cease at a point down the column where the resistance to the bubble's expansion was equal to its excess of tension. In this way Schwendener (1893) thinks it likely that the diminished tension in the vessels might be able to lift some water as much as 15^m instead of the 10^m to which a pressure of one atmosphere could lift an unbroken column. Under certain imaginary conditions, which as Schwendener showed do not really occur in plants, a much greater height would be possible; Schwendener (1892:934) suggests such a case in which the bubbles should be 10^{mm} long, in which Steinbrinck (1894:127) showed that the top of the column might be lifted 142^m . As to the actual length of the bubbles, Schwendener puts the average in *Fagus* at 0.33^{mm} , that of the supported water being 0.14^{mm} . Both Schwendener and Steinbrinck seem to assume in their calculations that a meniscus will retain its full effectiveness in a vacuum, which, as has just been pointed out, is not at all the case. Moreover, such a mechanism, in lifting water, would accumulate air at the top, and so destroy itself, and therefore (Askenasy, 1895), even if it could lift water once, it could not raise a constant stream.

During the last decade surface tension has been playing a very prominent part in still another form in explanations of the ascent of sap. The cohesive power of pure water was demon-

strated by Naegeli and interpreted with an insight in advance of his time. He says (1866: 498) "Viele Versuche zeigten, dass in frisch gezogenen Capillarröhren die Spannung negativ werden kann, ohne dass in dem ausgekochten Wasser Dampfbildung eintritt;" thus in one experiment the cohesion of the water sustained a mercury column 44^{mm} in excess of that in the barometer. Two other sentences outline Naegeli's interpretation: "Dieses Entzweireissen einer Wassersäule ist im Grunde nichts anderes als Dampfbildung in derselben⁵;" and concerning the amount of resistance to such pulling apart, "Es wäre selbst möglich, das es dafür keine Grenze gäbe." Böhm cites Helmholtz on this same point, the passage referred to (1874: 492) being on cohesion by very dilute sulphuric acid. Böhm himself in 1890 (Bot. Centralb. 268) found that *Salix* with boiled roots would absorb water and draw up mercury "Stets bis zur Barometerhöhe," when the total pressure of mercury in the water must have been above one atmosphere. Strasburger (1891: 792) got the same result with branches of *Taxus* and *Tsuga*. Böhm then (1893: 209) reported the lifting of mercury columns 22^{mm} above that of the barometer by *Salix*, and 161^{mm} above it by *Thuja*. In this paper Böhm seems to refer repeatedly to cohesion when he speaks of capillarity.

A little later than this, Askenasy (1895) published an exceedingly clear theory on the ascent of sap, in which the chief rôle in making the pull set up by evaporation in the leaves operative at indefinite distances down the trunk was ascribed to the cohesion of the water. The priority of the publication of most of this theory belongs to Dixon and Joly, who published abstracts of their work in 1894. The general acceptance of it is due more largely to Askenasy, whose name is usually associated with it. So is Strasburger's name, though he has not publicly subscribed to it, and it is not in harmony with all of his work. Like the imbibition theory, this one was complete in that the premises, proven and assumed, were an adequate foundation for the conclusion; the factors, as the theory used

⁵Physicists are not agreed on this.

them, were equal to their work. Its acceptance was naturally prompt and widespread, giving a new interest to the study of the cohesion of water from the physical side. Askenasy (1896: 441) was able to draw up mercury 82^{cm} and again 89.3^{cm} by a pull resulting from evaporation from a plaster of Paris surface. Dixon and Joly (Trans. Roy. Soc. 1895: 570), by a method better calculated to indicate very great tensions, demonstrated that columns of water could endure a longitudinal pull of more than seven atmospheres before breaking, and that this was possible without absolute freedom from gas, and with bits of *Taxus* wood in the water. By the same method Berthelot had obtained negative tensions, since variously estimated at 50 to 150 atmospheres. There is a résumé of some other work, including some of Lehmann's own, in his *Molecularphysik* (I: 243-5), in which Naegeli is overlooked. Kamerling (1898: 465) showed on theoretical grounds, the same as Naegeli's must have been, that in pure water *at rest* the resistance to pull must be infinite.

The supposed difficulty with other theories which the cohesion theory sought to overcome was their failure to provide for the transmission of really negative tensions, *i. e.*, tensions more than one atmosphere less than the normal. So long as the tension remains positive there is no possibility of the exercise of cohesion; the least positive tension would itself prevent a rupture of a column, whether of water or of water and air. But it is argued that water can be lifted 10^{m} at most while its tension remains positive; that when it is lifted higher, as in trees everywhere, negative tensions *must* be present near the top. There are two easy ways of determining empirically the opportunity for the play of cohesion in the plant: measuring the tensions actually present, and testing the result of artificially established tensions.

We have already mentioned that the tension of the air is ordinarily less than one atmosphere, and of course that of the contiguous water is the same. Well known to older writers, but too little considered, this fact came strongly to the fore with v.

Höhnel's work (1879). He found (p. 113) that a suction of 40–50^{cm} Hg was not rare as late in the year as the end of October. Böhm (1877) found a suction by *Crataegus* of 61^{cm}; by *Syringa* and some *Pomaceae* of 25^{cm}; and by *Platanus* of only 16^{cm}; and (Bot. Zeit. 1881: 824) even in March a suction by *Crataegus* of 40^{cm}. In one experiment (Bot. Zeit. 1881: 819) mercury was jerked into a vessel of *Robinia* 117^{cm}, but this was not a rise of that distance.

In 1890 Böhm said that *Salix* with boiled roots would exert a suction sufficient to lift mercury, as already quoted, "Stets bis zur Barometerhöhe." In 1893 he said that it was in "successful" experiments that the mercury could be drawn as high as the barometer by shoots whose lower end had been cooked; but only three experiments in 400 succeeded. In one of these three the indicated suction was 2.2^{cm} over an atmosphere. We have already noted his results with conifers. Strasburger (1891: 787) reports as the greatest observed suction in any herb 28^{cm} Hg (*Amaranthus caudatus*); in live branches of dicotyledonous trees, 54^{cm}; in branches whose lower end was boiled, 67^{cm}; and in conifers similarly treated, 70^{cm}. Vines (1896) reported suctions of 116^{mm} and of 11 inches by *Helianthus annuus*, 320^{mm} by *Prunus Laurocerasus*, 21¼ inches by *Fagus sylvatica*, and 22¼ inches by *Taxus*. These pressures are to be subtracted not from zero, but from one atmosphere (Vines, Annals of Botany 10: 644). Data obtained by Th. Hartig, Schwendener (1886), and others, by inserting manometers in the trunks of transpiring trees, agree that tensions of zero are not closely approached. A part of these figures may be lower than they should be, because they only indicate the point at which air came out of the cut end of the stem and prevented the absorption of any more water.

On the other hand, figures obtained after removing air by boiling or sucking it out of the cut end are likely to be too high. There is no doubt that the transpiring cells could draw water from the tracheae in spite of an absolute pull; that tensions of zero or less are not transmitted and used to absorb water as

because the air in the tracheae expands until finally it closes them to the passage of water. Removing a part of the air makes a lower tension necessary for what is left to plug the tracheae and so permits more than the normally possible suction. I have illustrated this with a small branch of a greenhouse grown *Eucalyptus*, the cortex removed, inverted so that when any bubbles were drawn from the stem they could not stay in contact with it and prevent the absorption of more water. It was in air-tight connection with a tube 1^{mm} in diameter, full of water and standing in mercury. The mercury rose in one hour and fifteen minutes 101^{mm}, where it was stationary. This suction was increased to 191^{mm}, but drew air from the pith and wood, and fell slowly to 106^{mm}. A little air continued to be extracted, but the suction increased, until 52 hours after the experiment began it was 173^{mm}; and after 79 hours 235^{mm}. The rise of mercury had become very slow, and at this point a leak stopped the experiment. The young leaves, up to those more than half grown, were already becoming dry, though the cut end was, and had constantly been, in water. It is because the possible suction is chiefly a function of the air in the tracheae that Vines (1896: 538) finds that a large part of the leaves may be removed from a branch without much effect on the suction. For the same reason—because a part of the tracheae are closed—a suction of less than the greatest the transpiration stream can exert may nearly stop the absorption of water (Vesque, 1884; Strasburger, 1891: 788). It seems clear to me that the evidence we have warrants the conclusion that the tensions in the tracheae of living plants—at least of dicotyledons—in nature are never even approximately as low as zero.⁶

What happens if the tension is artificially lowered? Böhm (1864:546) put more than a hundred *Salix* cuttings in a vessel where the pressure against the absorbing ends was reduced to 8 to 10^{mm} Hg. The result was "Dass die Blätter nach zwei oder höchstens drei Tagen vertrocknet waren. Das Absterben

⁶This was treated as an established fact by Naegeli and Schwendener (1877: 380).

erfolgte in der Regel bei kleinen Reichbeblätterten Pflanzen schneller als bei grösseren wenig beblätterten," etc. Böhmer's conclusion (562), "Dass die zum Saftsteigen erforderliche Kraft von dem Luftdrucke geliefert werde," is equivalent to saying that an actually negative tension cannot be exerted to absorb the water. Vesque (1884), working with sound water cultures of oleander, found that the absorption became impossible when the tension was one atmosphere *minus* 63^{cm} Hg. Strasburger (1891:793), Scheit (1886, II), and Janse (1887:3-10) all agree that dicotyledons wilt if water is available under too low a pressure, and that the removal of nearly the whole atmospheric pressure always makes it too low. Saussure (p. 30 of Ostwald's *Klassiker* no. 16, p. 214 of original) describes a somewhat different experiment explicable in the same way; vessels containing plants with their roots in water were placed *in vacuo* and lived for weeks, and even grew, if protected from direct illumination. Under the conditions the plant was in an atmosphere saturated with water and did not transpire. Water may have diffused rapidly enough to supply the demands of what growth occurred in a "vacuum." In direct light the plants dried up, because the leaves became warmer than the air, and water evaporated from them and could not be replaced.

We have found not only that negative tensions do not occur in dicotyledons in nature, but that an artificial elimination of the positive tensions to which they are accustomed robs them of the power to absorb and elevate the transpiration stream. There have been some premises and *a priori* arguments for the cohesion theory which, for the sake of thoroughness, we will still consider. Berthelot says (p. 332-3) "À ce moment (when negative tension has been caused by cooling) le moindre choc ou broissement, la moindre vibration fait réparaître à l'instant, avec une sorte d'ébullition, un léger bruit et une secousse plus ou moins notable, le gaz dissous dans l'eau." Lehmann (p. 244), speaking of water under a tension of one atmosphere *minus* 1,200 ^{mm} Hg, says "Erst bei erschütterungen folgt in solchen Fällen das Sinken zum normalen Standpunkt." Donny seems to be

alone (according to Lehmann) in reporting that a jar did not instantly release any negative tension, and his tension was only that of one meter of water. Trees are almost never absolutely at rest; their very agitation by the wind has served once (Spencer) to explain the rise of water. Kamerling, in the same mathematical argument showing that the cohesion of pure water at rest is not limited, proves that the kinetic energy of moving water may easily pull it apart. The transpiration stream not only moves, but moves irregularly, which no negative tension could survive. Because trees are not at rest and the transpiration stream is in unsteady motion, we must regard any negative tension in it as *a priori* impossible.

While Dixon and Joly (1895:571) regard a continuous column of water as an essential assumption in their theory, and base it on Strasburger's statement that there is very little air in the youngest wood, Askenasy, adhering more closely to Strasburger, recognizes that the presence of some air is not an effective bar to the movement of water in the same tracheae, and seems to expect cohesion to operate around and past bubbles. I cannot see the possibility. We believe cohesion to depend on the fact that the first break in a column of water must be an infinitely small bubble, whose surface is a meniscus of infinitesimal radius and a correspondingly great surface tension. In the wood bubbles are present of a very appreciable size. When transpiration is most active, and cohesion is supposed to be most necessary, these bubbles stretch and become practically cylinders. Midway up its side the surface of such a bubble is very much nearer that of a cylinder than of a sphere. The surface tension of such a meniscus hardly deserves the name of capillarity; cohesion is out of the question. The low tension of the bubble still further depresses the surface tension.⁷

Capillarity and cohesion are usually names of manifestations of surface tension under different conditions. Applied to its

⁷In a glass tube open at one end, the shape of the meniscus itself is a function of the tension of the gas; in the case we are considering this is not quite true, because the shape of the tracheae helps to determine that of the bubble.

manifestation in the single fixed set of conditions we have in the tracheae, they are not distinguishable. Ten years ago Böhm alone imagined (publicly) that capillarity could play the leading rôle in the ascent of sap. It had been tried and found wanting. Then it was named cohesion and sprang at once into popular favor.

I have been assuming that the transpiration stream does not rise in tracheae entirely free of bubbles. The evidence for this is unlimited. It was formerly taken as an established fact, and the imbibition theory rested very largely upon it. Since this theory collapsed, Schwendener has shown again by most careful work that when transpiration is active continuous water "threads" are wanting. The experiments of Strasburger (1891: 681-6), on which Dixon and Joly rest their case, were obtained in this way: branches were cut, under water if possible, and left standing in shade or darkness for some hours, until they had all the water they would hold; then they were examined and the youngest wood, which is most active in conducting water, was found to "contain very little air," or "the air could be detected with difficulty." It is easy to substantiate this observation. The subject of experiment has absorbed all the water it can, with the help of the whole pressure of the atmosphere, so there is no opportunity for the demonstration of cohesion, however abundant and continuous the water. The experiment gives no clue to the water content and its distribution when transpiration is active and water less accessible, and cohesion might be of service. Hartig (1888) and Wieler (1888), among others, have shown conclusively that it is just in this youngest wood that the water content is exceedingly variable, dependent on the supply and demand. Von Höhnelt (1879: 126) found the lowest tension in the youngest ring. And an experiment of Böhm's, already cited, shows that in the case of Robinia, one of Strasburger's few dicotyledonous subjects, active transpiration leaves the vessel far from full of water. The following experiment hits the question squarely; it also covers the other question of movement past bubbles, on which a superfluous amount of evidence is not yet in print.

A young branch of *Eucalyptus globulus*, with ten pairs of expanded leaves, all horizontal, stood in water four hours. The xylem was then full of water, excepting the large pitted vessels which contained bubbles occupying about half of their volume. Both sides of the stem for 2^{cm} were cut away almost half through, leaving only a very thin strip, which was protected against desiccation with vaseline. The structure was so fine that in the outer part of the xylem only the pitted vessels were clear cut and individually distinct. The lower end of the branch was tied into a glass tube containing a little water over a meter of Hg, the other end of which tube was swung down so as to subject the cut end to a pressure of 9^{cm} Hg instead of 74^{cm} (the atmosphere). Within five minutes the water began to disappear from the pitted vessels, which were soon visibly empty. The spiral vessels (primary) were but little later losing their water; while it was more than half an hour before the lumina of the wood fibers became generally empty. During the first part of this time the cut end was in contact with water, the rubber tube connecting the plant with the glass tube being bent 180°, so that air escaping from the branch would not collect against it. The branch used up its stored water, then, not because other water was not at hand, but because it cannot absorb it when the pressure is only 9^{cm} Hg. After about fifteen minutes the subject was kept horizontal under the microscope and very likely water was no longer kept against the cut end. To this point the experiment showed that, as Strasburger found, while the conducting part of the wood fills with water when it may be absorbed under the full atmospheric pressure, its lumina become empty again when this pressure is removed. When the leaves are called upon to exert a great suction, the continuous threads of water whose cohesion might transmit it do not exist.

After the lumina became free of visible water, the suction was removed, and the branch set in water for three minutes. Then eosin was given drop by drop to the cut end. It was eagerly absorbed, showing that the lumina had not filled to any considerable extent with air from outside. Watching for the eosin with the naked eye, it was between four and five minutes before

I detected it in the thin strip; then it had traveled the whole length of it on one side of the pith, nearly the whole on the other. It was absolutely confined to the spiral (primary) vessels, next the pith, and was about equally distributed in three to five layers of these. Twenty minutes later, isolated vessels outside of these (not the pitted ones) were injected. It was exceedingly evident in these isolated vessels, as I had been able to make out quite unsatisfactorily in the inner spiral ones where the whole group was red, that columns of colored water were separated by bubbles. With a high magnification I was able in a few places, where the thickness of the wood did not interfere too much, to see a very distinct red film lining the wall and connecting the indices of red liquid. It must be remembered that these vessels were the first in their immediate neighborhood to carry the eosin. It seems to me that the conclusion is warranted that the bubbles are not an appreciable obstacle to the passage of the water. Strasburger describes exactly the same case.

To summarize the discussion of the cohesion theory: It is applicable only in explaining the transmission of negative tensions; but negative tensions do not occur, nor do the positive tensions present approach zero; the movement of water is prevented by artificially removing the normal positive tensions; if negative tensions could arise they would be immediately released as a result of the movement of the water and the agitation of the trees; more than an insignificant negative tension is impossible in the presence of free gas or a vacuum, as the only bar to the enlargement of the bubble is its surface tension, and this decreases with the pressure; when the tension is low and transpiration is active, there are bubbles in all water conducting elements.

[*To be concluded*].

A REVISION OF THE GENUS NEMOPHILA.¹

HARLEY P. CHANDLER.

(WITH PLATES II-V)

THE North American genus *Nemophila* is represented by fourteen species and four varieties. Two species belong to the southern states, one primarily to the Rocky mountains, and the remainder to the Pacific slope, principally California.

It is one of the genera in which the tendency to variation is very strong, and this has been the source of much error and confusion in classification. Many of the common species were described by Europeans who were innocent of field experience on the Pacific coast, and this quite naturally resulted in mistakes. The types of these species have not been easily accessible to American botanists and confusion has been worse confounded by their diverse interpretations of the meager published descriptions.

The present paper was undertaken in the hope first of clarifying the synonymy. To this end original descriptions have been freely consulted, some forty type specimens have been examined, and drawings of two types have been obtained from Europe. Exhaustive lists of acknowledged synonyms have not been introduced, but all disputed names and those of recent publication have received attention. The second and more important hope of the writer was to contribute something to our knowledge of the plants themselves, by a study of their variations in the field, as well as in the herbarium. The best way of expressing both classes of results seemed to lie in a revision of the genus.

Discussions of the various characters available for discriminating forms will be found in the remarks following the descriptions of certain species. Here it will suffice to say that the

¹ Contributions from the Botanical Laboratories of the University of California.

almost infinite variation makes an accurate limitation of species absolutely impossible; and most of the species as here described include a great variety of more or less inconstant forms. Were these all described they would fill a volume, but nothing would be gained thereby. Convenience should be the aim of classification, and this aim is most effectually defeated by the multiplication of uncertain species.

To avoid possible uncertainty in interpreting the descriptions, it should be said that measurements of leaves are given as including the petiole; but the outlines as including only the blade, except where there is a conspicuously tapering base.

The question of the relation of *Nemophila* to *Ellisia* is vital, but must be left for future consideration.

The writer is indebted to the following persons for assistance in the preparation of this paper, principally by the loan of specimens: Mr. and Mrs. T. S. Brandegee, Miss Alice Eastwood (for the California Academy of Sciences), Dr. J. N. Rose (for the United States National Museum), Mr. S. B. Parish, Mr. H. M. Hall, Mr. J. P. Tracy, Prof. W. R. Dudley, Mr. Leroy Abrams, Mr. J. G. Lemmon, Prof. Aven Nelson, Prof. C. V. Piper, Mr. W. C. Cusick, Mr. Thomas Howell, Mr. Geo. Hansen, Mr. M. L. Fernald, Prof. L. F. Henderson, Prof. A. J. Cook, Mrs. Mary H. Manning, Miss Winifred Paine, Mr. R. H. Platt, Mr. W. N. Suksdorf, and Mr. Ralph Hopping. Special acknowledgment is due to the members of the Department of Botany of the University of California, and particularly to Prof. W. L. Jepson, at whose suggestion the study was first undertaken and whose constant encouragement and advice have been invaluable.

KEY TO THE SPECIES.

Flowers 1^{cm} or more across (except no. 2).

Leaves (at least the upper) alternate; seeds less than 5.

Angles of stems and often veins of leaves beneath retrorsely prickly.

Petioles broadly winged and auriculate-clasping; flowers 1 to 3^{cm}
across - - - - - 1. *N. aurita*

Petioles not winged nor auriculate-clasping; flowers less than 1^{cm}
across - - - - - 2. *N. racemosa*

Angles of stems not prickly.

Branches 2 to 6^{dm} long; all but the earliest leaves alternate; corolla 1 to 3^{cm} across, blue - - - - - 3. *N. phacelioides*

Branches 0.5 to 2^{dm} long; only the upper leaves alternate; corolla 1 to 2^{cm} across, violet with whitish green-spotted center - 4. *N. Kirtleyi*

Leaves mostly opposite; seeds usually 5 or more.

Corolla white with a dark purple spot at the tip of each lobe; scales oblong, half free, rolled toward the filaments - 5. *N. maculata*

Corolla blue or white without a spot at the tip of each lobe.

Corolla deep or pale blue, often veined with deeper blue and dotted toward the center; scales mostly broad, wholly adherent or free at the tip; cotyledons spatulate - - - - - 7. *N. Menziesii*

Corolla white or pale blue.

Cotyledons spatulate; corolla-scales linear, wholly adherent.

8. *N. Menziesii atomaria*

Cotyledons with orbicular or oval blade; corolla-scales oblong or linear, part free - - - - - 9. *N. Menziesii integrifolia*

Flowers 1^{cm} or less across.

Corolla tubular or tubular-campanulate.

Corolla equaling or longer than the calyx.

Leaves opposite; seeds more than 1; Pacific coast.

Leaves oblong (rarely ovate) in outline, pinnately 5 to 7-lobed; corolla-scales linear, often reduced to hairy lines; seeds 2 to 12 (mostly 6 or 8) - - - - - 11. *N. pedunculata*

Leaves spatulate in outline, 3 to 5-toothed or -lobed at the tip, with cuneate base; corolla-scales small and lacinate, or obsolete.

12. *N. spatulata*

Leaves mostly ovate in outline, pinnately about 5-lobed, the upper 3 lobes confluent; corolla-scales minute, various.

Plant hispid; lobes of leaves usually sharp; peduncles mostly shorter than the leaves; Washington to the Coast ranges of California - - - - - 13. *N. parviflora*

Plant with softer, spreading pubescence; lobes of leaves more rounded, the lower sinuses shallower; peduncles mostly exceeding the leaves; foothills of the southern Sierra Nevada.

14. *N. parviflora quercifolia*

Leaves alternate, mostly triangular-ovate, 3 to 5-lobed; seeds mostly 1 or 2; southern U. S. - - - - - 15. *N. microcalyx*

Corolla mostly shorter than the calyx; leaves mostly alternate; seeds 1.

16. *N. breviflora*

Corolla open-campanulate or pelviform.

Leaves opposite, oblong in outline, with 5 to 7 oblong lobes pinnately arranged; corolla mostly open-campanulate, not hairy within; scales linear, often reduced to hairy lines - - - - - 10. *N. sepulta*

Leaves opposite, spatulate, elliptical or lanceolate in outline, shallowly 3 to 5-lobed at the tip or entire; corolla mostly open-campanulate, often hairy at the center; scales oblong to linear, often half free, or reduced to hairy lines - - - - - 6. *N. humilis*

Leaves, especially the upper, sometimes alternate, typically with 5 to 9 suborbicular petiolulate pinnately arranged lobes, but very diverse; corolla mostly pelviform, not hairy within.

Calyx-appendages evident; corolla white or bluish; scales various.

17. *N. exilis*

Calyx-appendages minute or obsolete; corolla usually deep blue; scales linear, ciliate - - - - - 18. *N. exilis pulchella*

1. *N. AURITA* Lindl., Bot. Reg. t. 1601. 1833.—Plant weak and straggling, leaning on other plants for support: branches 2 to 6^{dm} long, hirsute, angled or winged, the angles armed with sharp prickles which aid in climbing: cotyledons not seen: leaves all but the lower alternate, 5 to 15^{cm} long, more or less deeply pinnatifid into mostly 7 to 13 entire or shallowly lobed downward-pointing divisions; retrorsely barbed along the principal veins beneath; petioles winged, expanded below into an auriculate-clasping base: flowers mostly in very loose naked racemes at the tips of the branches: calyx-lobes lanceolate, 4 to 10^{mm} long; appendages usually less than a third as long, spreading: corolla with a short throat constricted below the top and spreading limb 1 to 3^{cm} across, violet, paler outside; scales triangular, usually fimbriate, below covering the base of the stamens, above turning away from them, often 3^{mm} long: nectaries prominent, one between each pair of scales: style 2 or 3 times as long as the ovary, cleft only at the tip: capsule globular, 5 to 9^{mm} in diameter, thin-walled: seeds 4 per capsule, globular, 1.25 to 3^{mm} in diameter, conspicuously favose-reticulated; caruncle none (?).

The whole plant is prickly, sometimes even to the calyx.

CALIFORNIA AND ARIZONA.

Specimens examined: CALIFORNIA: Plumas co., Mrs. Austin; Stockton, Sanford no. 188; Kaweah river basin, Hopping no. 41, Woolsey; Bear creek, Tulare co., Purpus no. 1298; Kernville, Brandegee; Niles, Hall no. 1648; Palo Alto, Dudley; Bixby creek, Monterey co., Brandegee; Monterey co., McLean, Plaskett; San Luis Obispo, Lemmon; Dos Pueblos,

Santa Barbara co., *Brewer* no. 396; Casitas pass, Ventura co., *Hall* no. 3136; Santa Cruz island, *Brandeggee*; Fort Mojave, *Lemmon*; Los Angeles, *Hasse*; Santa Monica cañon, *Barber* no. 53; Fallbrook, San Diego co., *Hall* no. 515; Del Mar, San Diego co., *Brandeggee*.

ARIZONA: Diamond creek cañon, *Norman C. Wilson*.

The type was probably raised from seed sent by Douglas, who collected principally at San Francisco and Monterey, and is most likely in the herbarium at Kew or at the British Museum.

2. *N. RACEMOSA* Nutt., in Gray Proc. Am. Acad. 10: 315. 1875.—Near *N. aurita*, but less prickly: cotyledons with orbicular blade and long petiole: the leaves shorter and broader in outline and with fewer divisions, these more often toothed or lobed; petioles never broadly winged nor auriculate-clasping: flowers less than 1^{cm} across, more plainly racemose: corolla-scales narrow, often half free, sometimes obsolete.

SOUTHERN AND LOWER CALIFORNIA.

Specimens examined: CALIFORNIA: Santa Cruz island, *Brandeggee*; San Clemente island, *Nevin & Lyon*; Cajon heights, San Diego co., *Eastwood*; Del Mar, San Diego co., *Brandeggee*; San Diego, *Alderson* no. 1007, *Brandeggee*, *Setchell*.

LOWER CALIFORNIA: Guadalupe island, *Anthony* no. 254, *Brandeggee*, *Francheschi* no. 32, *Greene*; Cedros island, *Brandeggee*; San Martin island, *Anthony* no. 229, *Brandeggee*; Estaban, *Brandeggee*.

Type locality, "California; San Diego, Nuttall. Island of Catalina, Dall & Baker."

3. *N. PHACELIOIDES* Nutt., Jour. Acad. Philad. 2: 179. 1822.—Plant weak: branches 2 to 6^{dm} long, spreading- or retrorse-hirsute: cotyledons not seen: all but the earliest leaves alternate, pinnately divided into 3 to 9 oblong, oval, or obovate, 2 to 5-cleft divisions, the upper three divisions confluent, the others often distant: lower flowers terminal (though apparently axillary), the upper loosely racemose: calyx-lobes lanceolate or oblong, 5 to 10^{mm} long; appendages ovate or oblong, about half as long, not reflexed: corolla pelviform, 1 to 3^{cm} across, blue; scales broad, sometimes part free, fimbriate: style twice as long as the ovary, cleft for a third its length: capsule about 5 to 9^{mm} in diameter: seeds 4 per capsule, "obscurely compressed-punctate," according to Gray.

Only very scanty material of this species was accessible.

ARKANSAS AND TEXAS.

Specimen examined: TEXAS: Waco, Miss S. A. Trimble.

Type locality, Arkansas.

4. *N. KIRTLEYI* Henderson, Bull. Torr. Bot. Club 27: 350. 1900.—Plant weak, diffuse: stems 5 to 20^{cm} long, often purplish, hispid with spreading or retrorse hairs: cotyledons spatulate: upper leaves alternate, lower ones opposite, all triangular-ovate in outline, pinnately parted into usually five oblong or ovate, entire or 1 or 2-toothed divisions: peduncles exceeding the leaves: calyx-lobes lanceolate, 4 to 8^{mm} long, enlarging in fruit, minutely pubescent and long-ciliate; appendages lanceolate to ovate, a third as long or less: corolla pelviform, little exceeding the calyx, 1 to 2^{cm} across, "with violet border and whitish center, conspicuously green-spotted near the junction with the stamens;" scales broad, trapeziform, strongly fimbriate on the free edge: style nearly twice as long as the ovary, cleft for a third of its length: capsule globular or slightly elongated, 4 to 7^{mm} in diameter: seeds 2 to 4 per capsule, ovoid, 2 to 3^{mm} long, deeply pitted, the pits covered with deciduous scales; caruncle cap-like, evanescent.

IDAHO AND EASTERN OREGON. May be looked for in northeastern California.

Specimens examined: IDAHO: Florence, Henderson no. 3082 (co-type).

OREGON: Pine creek, Cusick.

The type locality is Salmon river hill, beyond Florence, Idaho county, Idaho, and the type specimen is in the National Herbarium.

5. *N. MACULATA* Benth., Jour. Hort. Soc. Lond. 3: 319. 1848.—Branches ascending or decumbent, 10 to 30^{cm} or more long, from almost glabrous to strongly hispid: cotyledons spatulate: leaves opposite, the lower 3 to 5^{cm} or more long, pinnately parted into 5 to 9 ovate or sub-orbicular, mostly 1 to 3-lobed divisions; the upper shorter, usually with but 3 or 5 entire lobes at the tip and a cuneately tapering base, or lanceolate and entire: peduncles surpassing the leaves: calyx-lobes oblong-lanceolate to ovate, 4 to 10^{mm} long; appendages lanceolate to linear, one fourth to one half as long, reflexed: corolla pelviform, 1 to 4^{cm} across,

much exceeding the calyx, white with a dark purple spot at the tip of each lobe and rows of purple dots radiating from the center; scales oblong to oblong-linear, half free, mostly rolled toward the filaments, ciliate, 2 to 3 mm long: style cleft about a third its length, 2 or 3 times as long as the ovary: capsule globular, 3 to 10 mm in diameter: seeds usually 5 to 12 per capsule, globular or slightly elongated, 1.5 to 3 mm long, sparingly pitted, scaly.

This *Nemophila* shows three types of leaf and they are not infrequently all found on one plant. The lowest leaves are deeply pinnate, resembling those of *N. Menziesii*; the next are shallowly lobed at the very tip, and have a long cuneate base; while those at the ends of the branches are often lanceolate and entire. The second form is the most common and characteristic. Depauperate specimens are not rare. The original collector called the plant *Nemophila speciosa*, but this name was not published with a description.

SIERRA NEVADA MOUNTAINS, MOSTLY BETWEEN 2,000 AND 5,000 FEET ALTITUDE.

Specimens examined: CALIFORNIA: Forbestown, Butte co., *E. Brooks*; Penn valley, Nevada co., *Jepson*; Placer co., *Bolander* nos. 4551 and 4566; Rose springs, El Dorado co., *M. H. Gates*; Clinton, Amador co., *Hansen* no. 88; Calaveras Big Trees, *Brewer* no. 2098, *Brandegee*, *Greene*; Pine ridge, Fresno co., *Hall & Chandler* no. 167; Kaweah river basin, *R. Hopping* no. 138; Mineral King and Coburn mills, Tulare co., *Brandegee*; Tulare co., *Purpus* nos. 1732, 3059, and 5706.

The type was raised in England from seed collected by Mr. Hartweg on an excursion "along the right bank of the Chuba [Yuba] river to the mountains [Sierra Nevada]." It is probably in the herbarium at the Royal Gardens, Kew.

6. *N. HUMILIS* Eastwood, Bull. Torr. Bot. Club 28: 150. 1901.—*N. Congdoni* Eastwood, *l. c.* 151.—In vegetative characters resembling *N. maculata*: leaves spatulate, elliptical, or lanceolate in outline, like the middle and upper leaves of that species: peduncles about as long as the leaves: calyx-lobes only 2 to 5 mm long; the appendages a third as long: corolla open-campanulate, 5 to 10 mm across, without a purple spot at tip of each lobe, but often with purple dots toward the center; scales from broad, lacinate and often half free to mere hairy lines which are often obscured by a mass of loose hairs at the center of the corolla: style once to twice as long as the ovary.

The available material of this species is unsatisfactory and it needs study in the field. Its affinity seems to be closest with *N. maculata*, from which it is readily distinguished by its smaller flowers, destitute of the purple spot at the tip of each corolla-lobe. It inhabits higher altitudes than that species.

SIERRA NEVADA MOUNTAINS FROM MARIPOSA COUNTY NORTHWARD.

Specimens examined: CALIFORNIA: Emigrant gap, Placer co., *M. E. Jones*; Summit, Placer co., *Eastwood* (type); Deer Park inn, Placer co., *C. J. Fox, Jr.*; Tioga road and Hetchy Hetchy road, Tuolumne co., *Congdon*; Hogan mt. and Konitz's place, Mariposa co., *Congdon*.

Type in the herbarium of the California Academy of Sciences, San Francisco, collected "on the trail between Summit and Summit Soda springs, in Placer county, June 9, 1898," by Miss Alice Eastwood, who states that it grew on a bank where the ground was still wet from the recently melted snow.

N. MENZIESII H. & A., Bot. Beech. Voy. 152. 1833, not of Syn. Fl., Bot. Cal., etc.—*N. insignis* Benth., Trans. Hort. Soc. n. s. 1:479. 1835. *N. liniflora* F. & M., Sert. Petrop. fol. & t. 8. 1846. *N. heterophylla* F. & M., l. c. *N. modesta* Kellogg, Proc. Cal. Acad. 7:93. 1877. *N. intermedia* Bioletti, Erythea 3:141. 1895. *N. Brandegei* Eastwood, Bull. Torr. Bot. Club 29:471. 1902. *N. macrocarpa*, Eastwood, l. c.—Branches slender or stout and succulent, ascending, mostly 10 to 25^{cm} long, more or less hirsute-pubescent with spreading or appressed, not always retrorse hairs: cotyledons usually spatulate: leaves mostly opposite, the lower 4 to 9^{cm} long, pinnately divided into 5 to 9 oblong, ovate, or suborbicular, mostly 2 or 3-lobed or -toothed divisions; upper leaves reduced and less divided in proportion to their distance from the root: peduncles slender, spreading, usually twice as long as the leaves: calyx-lobes lanceolate or ovate-lanceolate, 4 to 10^{mm} long; appendages lanceolate to linear, half as long or less: corolla pelviform, divided about three-fourths the way to the base, 1 to 3.5^{cm} across, from light to deep blue, veined deeper blue or purple, lighter-colored and often dotted, but seldom hairy toward the center; scales varying from broad and wholly adherent to narrow and part free, lacinate, ciliate or entire, often crisped: style 2 to 4 times as long as the ovary, parted for about a third its length: capsule elongated-globular, 5 to 10^{mm} in diameter: seeds 5 to 25 per capsule, 1 to 2^{mm} long, oblong-

ovoid or globose, scaly, rough, with a few deep pits; caruncle stipe- or cap-like.

Commonly called "baby blue eyes." Like all other *Nemophilas*, this species is exceedingly variable and sufficient allowance has not been made for the fact by some authors. It is particularly susceptible to moisture conditions. Where the soil is wet we find a succulent plant with sparse pubescence; where it is merely damp these characters are less pronounced; and where it is very dry the other extreme is reached—a very slender plant with dense pubescence. The variations in color are also striking (see note to the variety *atomaria*). Near the foggy coast of northern and central California the flowers are pale blue, usually dotted toward the center; in the Sacramento and San Joaquin valleys and in the sunny south coast ranges a deeper color predominates; while in southern California, which is practically desert except where reclaimed by man, a still more intense color is found. This is in accord with the common observation that in deserts flowers are brighter than in moister, less sunny regions; and since there are no accompanying variations which are at all striking, there seems to be sufficient reason for regarding as one species what a lay observer might distinguish as several different forms.

While mostly hermaphrodite, flowers with sterile anthers are occasionally found. They are smaller and deeper-colored than the others and according to Miss Alice Eastwood² they are associated with a more robust habit in the plant. Her investigations indicate that there is no marked difference in the seed-producing qualities of the two sorts of flowers.

There has been much confusion in the application of the specific names *Menziesii* and *insignis*, and the writer has investigated the matter with some care. The *Botany of Beechey's Voyage* was issued in parts. Page 152, on which the description of *N. Menziesii* appeared, is in Part 4, issued in 1833,³ two years before the publication of *N. insignis*. On page 372 (Part 8, 1840) an expanded description is given and two forms, α and β , are noted: " α . corolla calycem vix duplo superante" is stated to be the form described on page 152; " β . corolla calycem plus duplo superante" is given as equivalent to *N. insignis*, which had been published in the time between the issuance of pages 152 and 372. Hooker and Arnott, then, who were co-workers with Bentham and probably had seen the type *N. insignis*, found nothing to distinguish that species from *N. Menziesii* except a slight difference in the relative size of corolla and calyx, a character in which the field student of these plants cannot but recognize considerable variation. Indeed, Hooker once declared that *N. insignis* ought to be called *N. Menziesii*.⁴

² Erythea 3: 152.

³ See Jackson, in Journal of Botany 31: 298.

⁴ Bot. Mag. t. 3774.

As for the original descriptions, each easily includes the other. The only possible remaining ground for separating the two species lies in the fact that Hooker and Arnott describe their plant as having leaves precisely like those of *N. parviflora*. There is no large-flowered species which has leaves of that style except *N. phacelioides*, with which they were well acquainted and which does not grow in the same part of the continent as *N. Menziesii*. Moreover, had the leaves been essentially different from those of *N. insignis*, Hooker and Arnott would surely have made note of the fact in contrasting forms α and β .

These considerations seem to the author to establish the identity of *N. insignis* with *N. Menziesii*, and the priority of the latter name.

Dr. Fischer de Waldheim kindly sent to the Herbarium of the University of California a flowering branch from the type specimen of *N. heterophylla*. An examination of this and a consideration of the original description (which, by the way, it contradicts in having the upper leaves always opposite and never sessile) show that it is one of the countless forms of *N. Menziesii* (not of *N. parviflora*, as Gray and others have thought). *N. liniflora* is another of these forms. Had Fischer and Meyer themselves collected in California, they would have known better how to allow for variation in *Nemophila*.

In the expanded description of *N. Menziesii* referred to above, we find "corollae (caeruleae parce nigro-punctatae) . . ." If the corolla is dotted, it is probable that the type is the form most common in the north coast ranges of California, namely, that which Mr. Bioletti has separated as *N. intermedia*. But such a consideration aside, *N. intermedia* is not a good species (see above and note to *N. Menziesii* var. *atomaria*).

THROUGHOUT CALIFORNIA, EXCEPT IN THE NORTH AND THE HIGH MOUNTAINS.

Specimens examined: CALIFORNIA: Ukiah, Purdy; Mendocino co., Chandler; Ft. Ross, Davy no. 1673; Adobe cañon, Sonoma co., Michener & Bioletti; Santa Rosa cañon and Kenwood, Sonoma co., M. S. Baker; Vacaville, Jepson, Platt; Mt. Tamalpais, Chandler no. 281; Angel island, San Francisco bay, Michener & Bioletti; Oakland, Brewer no. 2764, Holder no. 2520; Berkeley, fresh material; Briones hills, Contra Costa co., Chandler no. 595; Bryants, Contra Costa co., Chandler no. 575; Moraga valley, Contra Costa co., Hall no. 1624; Mt. Diablo, Chandler no. 970; San Francisco, Chandler, Davy no. 2975, Jepson, etc.; Palo Alto, Dudley; Tres Pinos, Dudley; Pajaro hills, Monterey co., Chandler no. 410; Monterey, Plaskett; Pacific Grove, Chandler; San Luis Obispo co., Brewer no. 406, Mabel M. Miles no. 146; Santa Barbara, Brandegee; Santa Susanna mts., Brewer no. 216; Leonis valley, Davy no. 2610; Claremont, Martha Allen, Chandler; San Bernardino, Parish no. 25, Setchell; Gavilan, Riverside co., Hall no. 2931; Winchester, Hall; Temescal mts., Hall no. 406; San Jacinto, Mrs. Gregory; San Jacinto mts., Hall; Temecula, Cleveland; Banner, Brandegee;

Santa Ysabel, *Alderson*; San Felipe, *Brandege*; Rosedale, *Abrams*; Lerdo, *Brandege*; Tulare, *Davy* no. 3102; Kaweah, *R. Hopping* no. 166; Grapevine spring, Tulare co., *Woolsey*; Alcalde, *Brandege*; Fresno, *Buckminster*; Yosemite, *Dodd*; Rose springs, El Dorado co., *M. H. Gates*; Sacramento, *M. S. Baker*; Penn valley, Nevada co., *Jepson*; Sutter co., *Jepson*; Chico, *Winifred Paine*; "California," *Thomas Bridges*, no. 170.

The type was collected in California by the botanists of the Beechey Voyage, all of whose collecting was done at San Francisco and Monterey. It is in the herbarium at the Royal Botanic Garden, Kew, and is said to have no flowers.⁵

8. *N. MENZIESII atomaria* (F. & M.) Chandler, comb. nov.—*N. atomaria* F. & M., Ind. Sem. Hort. Petrop. 2:42. 1835. *N. Menziesii* of Bot. Cal., Syn. Fl., etc., not of H. & A. *N. insignis atomaria* (F. & M.) Jepson, Fl. West. Mid. Cal. 434. 1901. *N. venosa* Jepson l. c. (a garden escape). *N. Johnsoni* Eastwood, Bull. Torr. Bot. Club 29:472. 1902.—More succulent and less pubescent than the type, often nearly glabrous: calyx-lobes shorter and broader: corolla rather smaller, somewhat more deeply divided, white or pale blue, dotted or rarely only veined dark blue-purple or black, hairy at the center; scales very narrow, usually hairy, scarcely or not at all enlarged or free at the tip, often reduced to a mere line of hairs.

Some authors find the style more deeply divided than in the type.

This variety intergrades with the type in every character and the variations are not always concomitant, so that there are frequently specimens (e. g., *Chandler* no. 1276, Humboldt co., Cal.) which may be referred almost equally well to either. Plants which in every other respect answer to var. *atomaria* (e. g. *Michener & Bioletti*, Sonoma, Cal.) have scales broader than is usual even in the type; while others which are plainly *N. Menziesii* (e. g., *Plaskett*, Monterey, Cal.) have the scales reduced to a mere line of hairs. Between these extremes there is every variation.

In a series of a half dozen living specimens from Kenwood, Cal., *M. S. Baker*, there were several instructive series. In color and marking of corolla three distinct steps were observed on as many plants: *A*, flowers white, dotted with blue to the edge; *B*, flowers slightly bluish, veined deeper blue, dotted toward the center; *C*, flowers bright blue, veined darker blue, white (but not dotted) at center. In the matter of succulence, a series of three plants showed a decided increase of pubescence and an approximately corresponding decrease of succulence as the type was approached. The shape of the calyx-lobes varied less uniformly.

⁵ Bioletti, *Erythra* 3: 140.

A species is probably now being evolved in the direction of greater succulence, less pubescence, smaller and lighter-colored flowers, shorter calyxlobes and narrower corolla-scales; but on account of the complete intergradations and the frequent lack of concomitance in variation, it seems best to retain the form as a variety. For this same reason *N. intermedia*, which lies between *N. Menziesii* and the variety, is excluded.

Most of the variegated garden *Nemophilas* should probably be referred to this variety.

COAST RANGES OF CALIFORNIA, IN MOIST PLACES.

Specimens examined: OREGON: Elk Head, Douglas co., *Howell*.

CALIFORNIA: Smith river, Del Norte co., *P. E. Goddard*; Hupa, Humboldt co., *Chandler, Davy & Blasdale* no. 5739, *Mrs. Manning*; Ukiah, *Purdy*; Round valley, Mendocino co., *Westerman*; Napa river basin, *Jepson*; Yountville, *Jepson*; Sonoma, *Michener & Bioletti*; Kenwood, *M. S. Baker*; Cloverdale, *Setchell*; Point Reyes, *Davy* no. 1684, *Eastwood*; Olema, *Davy* no. 681; Fairfax, *Michener & Bioletti*; Mt. Tamalpais, *Chandler* no. 485, *Jepson*; San Francisco, *Chandler*, etc.; San Mateo co., *Tidestrom*; Loma Prieta mt., *Davy* nos. 441, 541, and 604; Alma, Santa Cruz co., *Brandegge*; Glenwood, Santa Cruz co., *Michener & Bioletti*.

The type locality is "circa coloniam Ross in Nova California," near the present town of Fort Ross. The type specimen is doubtless in the herbarium of the Imperial Botanic Garden at St. Petersburg.

9. *N. MENZIESII* INTEGRIFOLIA Parish, *Erythea* 6: 91. 1898.—*N. rotata* Eastwood, *Bull. Torr. Bot. Club* 28: 159. 1901. excl. pl. *Orcutt*.—Plants slender, often prostrate: cotyledons with orbicular or oval blade: leaves usually (not always) somewhat less divided than in the type, sometimes even entire or with only a few lobes at the tip and a cuneately narrowing base: peduncles sometimes shorter than the leaves: flowers smaller than in the type: corolla pelviform to almost rotate, often only 1^{cm} across, pale blue or white, veined blue, usually hairy and dotted with purple toward the center; scales oblong to linear, half free or attached by one of the narrow edges, variously hairy or lacinate.

The leaves of this variety are infinitely various and a great range of shapes is often found on the same plant. The scales are also various, but almost never wholly adherent; the most common form seems to be a linear scale which is attached for half its length, then turns outward at an obtuse angle and comes to a bristly acuminate point.

The var. *integrifolia* is a southern analogue of the var. *atomaria*, from which it differs chiefly in less succulent habit, greater pubescence, shape of

cotyledons, less divided leaves, peculiar corolla-scales, and geographical range. Where the ranges of the two varieties meet they intergrade (Leonis valley, *Davy*: Casitas pass, *Hall*).

Of the variety as described here, the type specimen is an extreme form, having mostly entire leaves.

SOUTHERN CALIFORNIA.

Specimens examined: CALIFORNIA: Elizabeth lake, Los Angeles co., *Hall* no. 3081; Antelope valley, *Davy*; Leonis valley, *Davy*; Pasadena, *M. E. Jones*; Santa Monica, *Barber*; Claremont, *Illingworth*, *Sanborn*; San Bernardino mts., *Hall*, *Parish* no. 4196; Palomar, *Hall* no. 1951; Ramona, *Brandeggee*; San Jacinto mts., *Hall* no. 2266; Encinitas, El Volcan, and Point Loma, San Diego co., *Brandeggee*; Witch creek, San Diego co., *Alderson*; Laguna woods, San Diego co., *Cleveland*; San Diego, *Eastwood* (type of *N. rotata*).

The type locality is Waterman cañon, San Bernardino mountains, and the type specimen is in the herbarium of S. B. Parish, at San Bernardino.

10. *N. SEPULTA* Parish, *Erythea* 7:93. 1899.—*N. Menziesii minutiflora* Suksdorf, *Deut. Bot. Monatsch.* 18:133. 1900. *N. densa* Howell, *Fl. N. W. Am.* 466. (Mch. 21) 1901. *N. nana* Eastwood, *Bull. Torr. Bot. Club* 28:151 (Mch 27) 1901. *N. exigua* Eastwood, *l. c.* 157. *N. alata*, Eastwood, *l. c.* 158.—Plant prostrate, or very rarely sub-erect: branches from mostly a few centimeters to 4^{dm} long, sometimes winged, sparingly pubescent: cotyledons spatulate: leaves opposite, 2 to 5^{cm} long, oblong in outline, pinnate into 5 to 7 mostly oblong, rarely toothed divisions: peduncles shorter or longer than the leaves, strongly deflexed in age and sometimes burying the capsules: calyx-lobes lanceolate, 2 to 5^{mm} long; appendages from a third to three-fourths as long, spreading or reflexed: corolla open-campanulate, the lobes longer than the tube, 3 to 7^{mm} across, white, often dotted with blue toward the center; scales linear or reduced to hairy lines: style from once to twice as long as the ovary, divided for a third or a half its length: capsule globose, 3 to 6^{mm} in diameter: seeds usually about 4 per capsule, irregularly elongated-globose, 2 to 3^{mm} long, coarsely pitted and minutely scabrous (when typical), scaly; the caruncle cap-like.
Plate I.

This species is very close to the succeeding and also shows affinity with

N. Menziesii. Field study is needed with reference to the shape and markings of the corolla.

FROM WASHINGTON TO SOUTHERN CALIFORNIA.

Specimens examined: WASHINGTON: Clark co., *Suksdorf* no. 2315; Klickitat co., *Suksdorf* nos. 684 and 2198 (co-type of *N. Menziesii minutiflora*).

OREGON: Mosier, Wasco co., *Howell*; Oregon city, *Howell*; Mitchell, Crook co., *Howell*; Prineville, Crook co., *Leiberg* no. 250; Ouryhee, Malheur co., *Leiberg* no. 2180.

CALIFORNIA: Little Shasta, Siskiyou co., *F. W. Hooper*; Forestdale and Pine creek, Modoc co. *M. S. Baker*; Clear creek, Butte co., *Brown* no. 173 (type of *N. alata*); Mohawk valley, Plumas co., *Lemmon*; Sierra valley, Sierra co., *Lemmon*; Stony creek, Amador co., *Hansen* no. 1522 (type of *N. exigua*); Bartlett mt., Lake co., *Eastwood* (type of *N. nana*); San Bernardino mts., *Parish* nos. 1842, 3782 (co-type), and 4908.

The type locality is Bear valley, San Bernardino mts., California, and the type is in the herbarium of Mr. S. B. Parish, at San Bernardino.

11. *N. PEDUNCULATA* Dougl., in Benth. Trans. Linn. Soc. 17: 275. 1837.—*N. humifusa* Kellogg, in Eastwood, Bull. Torr. Bot. Club 28: 41. 1901. *N. Austinae* Eastwood, l. c. 143.—Plant prostrate, in open places spreading in dense mats, or among underbrush decidedly lax: branches mostly 5 to 30^{cm} long, sparingly pubescent: cotyledons mostly with oval blade and narrow petiole: leaves opposite, 2 to 5^{cm} long (in rare cases 8^{cm} long), oblong (or rarely ovate) in outline, pinnate into 5 to 7 broad, usually toothed or lobed divisions: peduncles shorter (or sometimes longer) than the leaves, strongly deflexed in age and sometimes burying the capsules: calyx-lobes lanceolate, 1.5 to 4^{mm} long; appendages narrower, usually less than half as long, spreading or reflexed: corolla tubular or tubular-campanulate, the lobes about as long as the tube, scarcely exceeding the calyx, 2 to 3^{mm} across, white or pale blue; scales linear or reduced to hairy lines: style from once to twice as long as the ovary, divided for a third or a half its length: capsule globose, mostly 2 to 4^{mm} in diameter: seeds 2 to 12 (mostly 6 to 8) per capsule, elongated-globose, 1.5 to 2.5^{mm} long, coarsely pitted and minutely scabrous, scaly; caruncle cap-like, often having a narrow prolongation at one side. *Plate II.*

N. Austinae may prove distinct enough to become a variety. It is

marked chiefly by its often shallowly 5-lobed leaf, which is ovate in outline, and its few seeds (2 to 4 per capsule). The type came from Davis creek, Modoc county, California, *Mrs. Austin*, and specimens collected by the writer at Marble mountain, Siskiyou county, are similar. The form should be observed for other characters.

FROM WASHINGTON TO LOWER CALIFORNIA.

Specimens examined: WASHINGTON: Klickitat co., *Suksdorf* nos. 2637, 2638.

OREGON: Dalles city, *Suksdorf* no. 2639.

CALIFORNIA: Davis creek, Modoc co., *Austin* (type of *N. Austinae*); Marble mt., Siskiyou co., *Chandler* nos. 1649 and 1706; Susanville, Lassen co., *Brandeggee*; San Francisco, *Kellogg* (type of *N. humifusa*), *Chandler* no. 1800; Coyote creek, Santa Clara co., *Chandler* no. 929; Island of Santa Cruz, *Brandeggee*; Santa Inez mts., *Brandeggee*; Porterville, Tulare co., *Dudley*.

LOWER CALIFORNIA: Japa valley, *Orcutt* no. 1128, in part.

The type locality is the Columbia river and the type specimens are in the herbarium of the Royal Botanic Gardens at Kew.

12. *N. SPATULATA* Coville, Bot. Death valley. 156. 1893.—*N. inconspicua* Eastwood, Bull. Torr. Bot. Club 28: 144. 1901, not *N. inconspicua* Henderson. *N. pratensis* Eastwood, *ibid.* 29: 474. 1902.—Closely related to *N. pedunculata*, but differing in the following particulars: leaves spatulate in outline, 3 to 5-toothed or -lobed only at the tip, with long cuneate base: corolla often with a purple spot at the tip of each lobe and a few dots at the center; scales small and lacinate or obsolete: style sometimes scarcely evident: seeds fewer (mostly 3 or 4) per capsule; caruncle cap-like, without a prolongation at one side.

The type specimen is itself an intergrade and dangerously near *N. pedunculata*. At the other extreme the variation is toward *N. maculata*, which it approaches in leaves and corolla markings.

SOUTHERN SIERRA NEVADA AND SAN JACINTO MOUNTAIN, CALIFORNIA.

Specimens examined: CALIFORNIA: Sierra Nevada mts., Fresno co., *Hall & Chandler* nos. 104, 411 and 423; Bearskin meadow, South fork King's river, *Eastwood* (type of *N. inconspicua* Eastwood); Sierra Nevada mts., Tulare co., *Death valley expedition* nos. 1522 and 1671 (type); San Jacinto mt., *Hall* no 2406.

"Type specimen in the United States National Herbarium, no. 1671,

Death valley expedition; collected August 21, 1891, in Whitney meadows, Sierra Nevada, Tulare co., California, by Frederick V. Coville."

13. *N. PARVIFLORA* Dougl., in Benth. Trans. Linn. Soc. 17: 275. 1837.—*N. inconspicua* Henderson, Bull. Torr. Bot. Club 27: 349. 1900, not *N. inconspicua* Eastwood. *N. macrophylla* Eastwood, Bull. Torr. Bot. Club 28: 144. 1901. *N. pustulata* Eastwood, l. c. 145. *N. micrantha* Eastwood, l. c. 146. *N. Kelloggii* Eastwood, l. c. 147. *N. Plaskettii*, Eastwood, l. c. 147.—Stems mostly weak, decumbent or ascending, 3 or 4^{cm} to as many decimeters long, hispid: cotyledons with orbicular or oval blade and long slender petiole: leaves mostly opposite, 1 to 6^{cm} long, various but typically ovate in outline, pinnately 5-lobed, the lobes toothed or lobed, the upper three often confluent, the lateral occasionally petiolulate: peduncles seldom as long as the leaves: calyx-lobes triangular or lanceolate, 1 to 4^{mm} long; appendages less than half as long, lanceolate, spreading: corolla mostly tubular-campanulate, 2 to 5^{mm} across, little exceeding the calyx, white or suffused with blue; scales minute, various but usually half free and ciliate or lacinate: style once to twice as long as the ovary, divided about half way: capsule globose, 3 to 5^{mm} in diameter: seeds usually 4 per capsule, but varying from 2 to 5, irregularly globose, deeply pitted and minutely roughened, scaly; caruncle stipe-like. *Plate III.*

FROM IDAHO AND WASHINGTON THROUGH OREGON AND THE COAST RANGES OF CALIFORNIA.

Specimens examined: BRITISH COLUMBIA: Vancouver, *Macoun* (type of *N. pustulata*).

IDAHO: Soldier mt., *Henderson* (type of *N. inconspicua* Henderson).

WASHINGTON: Whidby island, Puget sound, *Gardner* no. 395; Nesqually, Puget sound, *Wilkes Exped.*, no. 90; Seattle, *Piper*; upper valley of the Nesqually, *Allen* no. 61; Klickitat co., *Suksdorf* no. 172; "Washington Territory," *Dr. Cooper*; "Washington," *Brandegee*.

OREGON: Portland, *Henderson*, *Kellogg & Harford*; Polk co., *Spillman*; "Western Oregon," *Howell*; Sauvie's island, *Howell*.

CALIFORNIA: Sonoma bar, Siskiyou co., *Chandler* no. 1537; Redwood creek, Humboldt co., *Chandler* no. 1270; Hydesville, Humboldt co., *Tracy*; Rowe's station, Mendocino co., *Chandler* no. 1037; Ukiah, *Purdy*; Mendocino, *Brown* no. 742; Inverness, Marin co., *Eastwood*; Mt. Tamalpais,

Chandler nos. 515, 769, etc., *Eastwood* (type of *N. micrantha*); San Mateo co., *Kellogg & Brannan*; Wrights, Santa Cruz co., *Brandegee*; Big basin, Santa Cruz mts., *Dudley*; Santa Cruz mts., *Kellogg & McLean* (type of *N. Kelloggii*); Santa Lucia mts., Monterey co., *Plaskett* no. 32 (type of *N. Plaskettii*); "California," *Vasey*.

The type locality is the Columbia river and the type specimen is in the herbarium at the Royal Gardens, Kew.

14. *N. PARVIFLORA quercifolia* (Eastwood) Chandler, comb. nov.—*N. quercifolia* Eastwood, Bull. Torr. Bot. Club 28:142. 1901.—Plant with softer, more spreading pubescence than the type: leaves with more rounded lobes and shallower sinuses, the lower of these scarcely deeper than the upper: peduncles mostly exceeding the leaves: calyx-lobes mostly oblong.

This variety is separated on what are usually rather unstable characters, but here they seem constant enough to warrant a separation, especially since the geographical range is quite remote from that of the type.

FOOTHILLS OF THE SOUTHERN SIERRA NEVADA.

Specimens examined: CALIFORNIA: Pine ridge, Fresno co., *Hall & Chandler* nos. 91 and 250; Sequoia mills, Fresno co., *Eastwood* (type); Kernville, *Brandegee*; Greenhorn mts., Kern co., *Palmer* no. 32; San Emidio cañon, Kern co., *Davy* no. 2070.

Type in the herbarium of the California Academy of Sciences, San Francisco; collected at Sequoia mills, Fresno co., by Alice Eastwood.

15. *N. MICROCALYX* (Nutt.) F. & M.—*Ellisia microcalyx* Nutt., Trans. Am. Phil. Soc. II. 5:191. 1833-7. *E. ranunculacea* Nutt., l. c. *Nemophila microcalyx* F. & M. Sert. Petrop. t. 8. 1846.—Near *N. parviflora*, but differing principally in the following particulars: leaves broader at the base, often only 3-parted, mostly alternate: peduncles shorter: corolla-scales often obsolete: seeds usually only 1 or 2 per capsule.

SOUTHERN UNITED STATES, FROM VIRGINIA AND FLORIDA WESTWARD TO ARKANSAS AND TEXAS.

Specimens examined: TENNESSEE: Knoxville, *Ruth*; Nashville, *A. H. Curtiss* no. 2125, *Gattinger*.

ARKANSAS: Little Rock, *Hasse*.

LOUISIANA: St. Martinsville, *Langlois*.

Type locality, "Arkansas, Alabama, etc."

16. *N. BREVIFLORA* Gray, Proc. Am. Acad. 10:315. 1875.—*N. parviflora* of Torr. in Wats. Bot. King Exp. 249, excl. char.—

Plant usually weak, though often fleshy: branches decumbent or ascending, 5 to 35^{cm} long, sparingly hairy: cotyledons spatulate: leaves (all but the lowest) alternate, 2 to 5^{cm} long, triangular-ovate in outline, deeply pinnately parted into mostly 5 oblong, falcate, entire or 1 or 2-toothed divisions: peduncles shorter than the leaves: calyx-lobes oblong- to linear-lanceolate, 2 to 5^{mm} long in flower, enlarging greatly in fruit, nearly or quite glabrous except for the strongly ciliate margins; appendages proportionately broader, less than half as long, reflexed: corolla mostly tubular, not exceeding the calyx, about 2^{mm} across, white or purplish; scales narrow, trapeziform, fimbriate: style scarcely longer than the ovary, cleft only at the tip: capsule globular, 3 to 5^{mm} in diameter: seeds 1 per capsule, globular, 2 to 3.5^{mm} in diameter, pitted and minutely roughened, scaly, often blood-red; caruncle cap-like (?), evanescent.

ROCKY MOUNTAINS FROM UTAH TO MONTANA AND WESTWARD TO WASHINGTON AND OREGON. Not yet found in California, but to be looked for in Modoc and Siskiyou counties.

Specimens examined: WASHINGTON: Yakima region, *Brandegee*; Falcon valley, *Suksdorf*; "Washington," *Vasey* no. 403.

OREGON: Blue mts., *Coville* no. 537, *Howell*; eastern Oregon, *Cusick*; Steins mts., *Leiberg* no. 2498.

MONTANA: Summit G. N. Ry., *Williams* no. 170; Bridger mts., *Rydberg* & *Bessey* no. 4860.

IDAHO: Coeur d'Alene mts., *Leiberg* no. 1062; Latah co., *Piper*; Craig mts., *Henderson* no. 2748.

WYOMING: Yellowstone park, *Nelson* no. 5566, *Tweedy* no. 405; Teton forest reservation, *Brandegee*.

UTAH: Bear river cañon, *Watson* (*King exped.*) no. 869 (type).

The type was collected at Bear river cañon, Utah, July, 1869, by Sereno Watson, as no. 869 of the Clarence King expedition, and was determined by Torrey (not by Watson, as Gray implies in his citations) as *N. parviflora*. It is in the United States National Herbarium.

17. *N. EXILIS* Eastwood, Bull. Torr. Bot. Club 28: 148. 1901. —*N. flaccida* Eastwood, l. c. 149. *N. inaequalis* Eastwood, l. c. 149. *N. hispida* Eastwood, l. c. 152. *N. divaricata* Eastwood, l. c. 153. *N. tenera* Eastwood, l. c. 153. *N. gracilis* Eastwood, l. c. 154. *N. nemorensis* Eastwood, l. c. 155. *N. glauca* East-

wood, *l. c.* 156. *N. fallax* Eastwood, *l. c.* 156. *N. diversifolia* Eastwood, *ibid.* 29: 473. 1902. *N. decumbens* Eastwood, *l. c.* — Plants when growing in deep shade weak and only moderately hairy; in more open places usually more stout and hispid: branches from a few centimeters to 6^{dm} long: cotyledons with orbicular or oval blade and slender petiole: leaves exceedingly diverse in form and size, 1 to 10^{cm} long; the lower opposite, mostly pinnate with 5 to 9 suborbicular, often 2 or 3-lobed divisions on narrow petiolules; the upper often alternate, less divided, not rarely entire: peduncles slender, shorter or longer than the leaves, spreading: calyx-lobes from ovate- to linear-lanceolate, 1.5 to 5^{mm} long; appendages proportionately broader, mostly less than a fourth as long, reflexed: corolla pelviform or broadly campanulate, 4 to 10^{mm} across, white or bluish; scales various, semicircular, oblong or triangular, occasionally half free, entire or lacinate: style from 1 to 3 times as long as the ovary, parted for from a third to a half its length: capsule globular, 2 to 4^{mm} in diameter: seeds 2 to 5 per capsule, elongated-globular, scrobiculate; caruncle cap- or stipe-like. *Plate IV.*

This species includes several forms which have long been classed with *N. parviflora*. It represents a larger range of variation than any other *Nemophila*, but these variations are nearly all directly referable to life relations. In view of the attempt which has recently been made⁶ to define several species in this group, a discussion of the characters employed in discrimination of the forms seems worth while.

Habit, pubescence, and leaves do not afford satisfactory characters, for they all depend to a great extent on the life relations of the individual. For example, plants growing in deep shade tend to produce broad leaves and sparse pubescence, the degree of dissection of the leaves and the density of the pubescence being fairly accurate measures of the intensity of the light received; moisture very strongly increases the general thrift of the plant and diminishes the pubescence; competition prevents spreading and lengthens the internodes; so, too, soil, temperature, wind, and a dozen other factors have their influences. When we remember that not one, but all of these factors are operative on each plant, and when we realize that we are dealing with one of the most unstable of genera, we are constrained to put little faith in vegetative characters.

⁶ EASTWOOD, Bull. Torr. Bot. Club 28: 137 *et seq.*

Miss Eastwood has divided the small-flowered *Nemophilas* into eight groups based upon the shapes of the corolla. These distinctions are too fine. Such factors as age, the time of day, the degree of shade, or the amount of nourishment received by the individual plant may easily make great differences in the appearance of pressed flowers. For example, in the morning a plant may appear to have tubular flowers, while in the afternoon, when the light is more intense, the same flowers may open wider and become tubular-campanulate. If pressed in the morning condition, the flowers even when soaked up will appear tubular, and correspondingly for those pressed in the afternoon condition. As an instance of how dangerous such a close division on this line may be, witness that Miss Eastwood has placed *N. sepulta* in Section 1, "Corolla tubular, minute," when that species almost invariably has open-campanulate flowers.

The position of the corolla-scales is also unreliable. In the living flowers of most species the scales stand nearly perpendicular to the corolla; so their position in the pressed flower is accidental, or at most represents a very slight inclination from the perpendicular in the living flower. One frequently finds in the same flower some scales folded towards the stamens and others folded away from them; so that in most cases very little significance can be attached to their position.

The shape of the scales is also exceedingly diverse, apparently much more so than in the large-flowered species. Plants which agree in every other particular often show quite different scales, and there is sometimes considerable variety on one plant or even in one flower.

The writer has found no character which seems perfectly satisfactory for discriminating species. In so variable a genus as *Nemophila*, and more particularly in this most variable group, concomitance in variation should be demanded before a form is named; otherwise there is no limit to the number of species we may make and our classification will become a burden. Some of the species here reduced may prove to present such concomitance when they are better known; but at present the writer does not feel justified in maintaining them.

Unfortunately, the type specimen of *N. exilis* is not a typical form of the species as here described. The writer does not find the corollas of the type "distinctly salverform," and he inclines to the opinion that their approximation to that form is due to the flowers shriveling before being pressed. Flowers of even so open-flowered a species as *N. Menziesii* have been seen where this had occurred with a similar result. If this character should prove to have value, however, and if it can be connected with other characters, the remaining forms should be separated as variety *flaccida*. Plate IV represents the form published as *N. nemorensis*, which is the most common one about San Francisco bay, and which is taken as typical of the group of forms which make up the species.

It is perhaps worthy of note that the leaves which are least divided are most often alternate. This tendency is shown on very many specimens, and is extreme in the forms separated as *N. flaccida* and *N. inaequalis*.

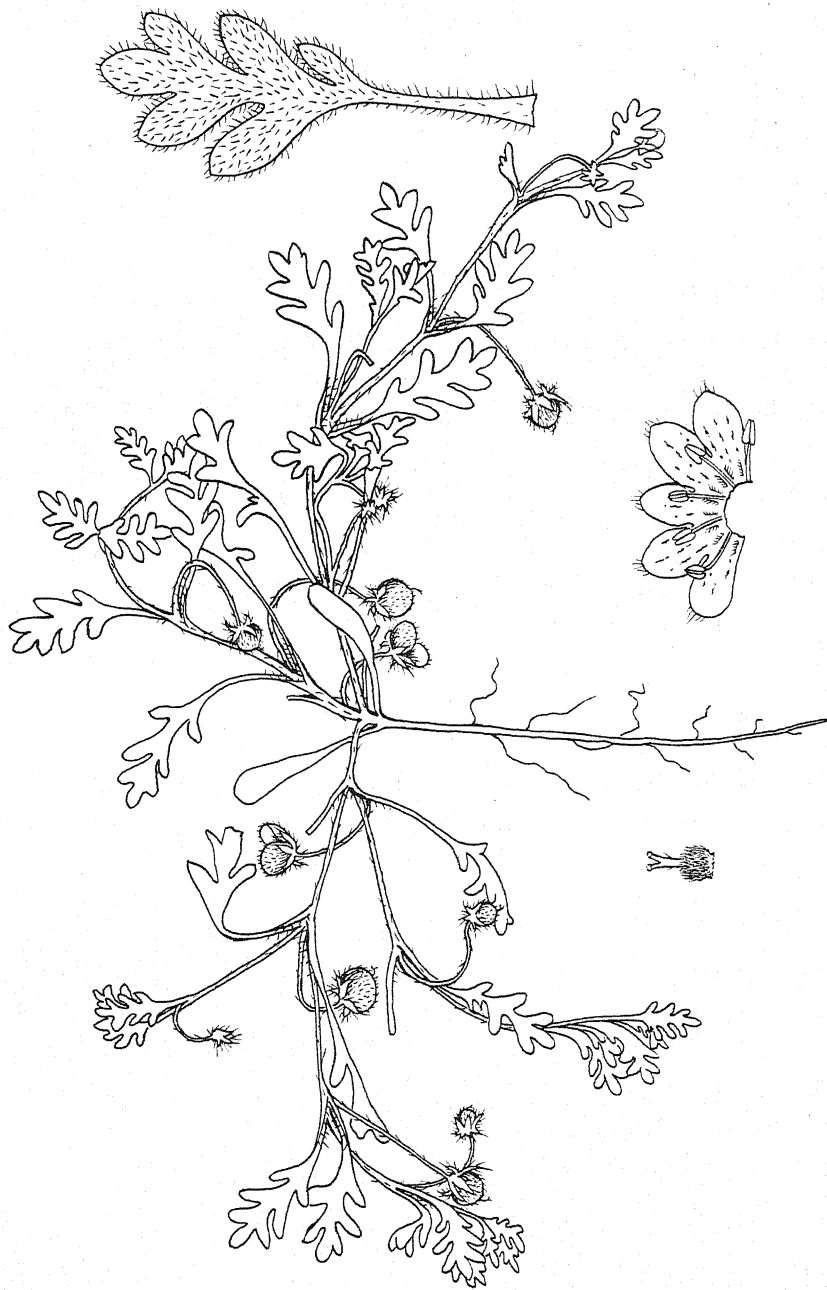
FROM SOUTHERN OREGON THROUGH NORTHERN AND CENTRAL CALIFORNIA.

Specimens examined: OREGON: Rogue river valley, *Howell*.

CALIFORNIA: Hupa, Humboldt co., *Mrs. Manning*; Mendocino co., *Bolander* no. 4647, *Brandegee*, *Chandler* nos. 1035 and 1065, *Eastwood*, *Purdy*, *Westerman*; Solano co., *Setchell*; Napa co., *Jepson*; Rutherford, *Chandler* no. 630; Sonoma co., *M. S. Baker*, *Bolander* nos. 3802 and 3811, *Samuels* no. 174; Windsor, *Mrs. Swett*; between Clear lake and Bartlett springs, *Eastwood* (type of *N. hispida*); Mt. St. Helena, *Eastwood* (type of *N. divaricata*); Russian river, *Brandegee* (type of *N. inaequalis*); Marin co., *Brewer* no. 938; Fairfax, *Eastwood* (type of *N. nemorensis*), *Michener & Bioletti*; Mt. Tamalpais, *Chandler* nos. 256, 768, etc., *Davy* no. 143, *Eastwood*, *Michener & Bioletti* etc.; Sausalito, *Kellogg & Harford* no. 785; Angel island, San Francisco bay, *Davy* no. 6885, *McLean*, *Michener & Bioletti*; Berkeley, *Chandler* nos. 554, 567, 1802, 1803, 1804, etc., *Davy* nos. 6920, 6922, etc., *Greene*, *Hall*, etc., and fresh material; Oakland, *Chestnut*, *Holder* no. 2589; Moraga valley, Contra Costa co., *Hall* no. 1625; Mt. Diablo, *Chandler* nos. 948, 949, and 985; Briones valley, Contra Costa co., *Chandler* nos. 580 and 580A; Antioch, *Davy* nos. 907 and 916; Martinez, *Chandler* no. 850; Stanford University, *Dudley*, *Rutter* no. 6; Loma Prieta mt., Santa Clara co., *Davy* no. 72a; Evergreen, Santa Clara co., *Davy* nos. 532 and 608; Pitt river, Shasta co., *Brown* no. 261 (type of *N. flaccida*); Iron cañon, Butte co., *Mrs. Austin* no. 272; Chico, *Winifred Paine*; Big Chico creek, *Austin* no. 2037 (types of both *N. glauca* and *N. fallax*); Stites, Colusa co., *Brandegee*; Applegate, Placer co., *Helen Smith* (type of *N. tenera*); Stockton, *Sanford*; Rose springs, Eldorado co., *Gates*; Amador co., *Hansen* nos. 1377 and 2064; Gwin mine, Calaveras co., *Jepson* no. 1785; Milton, Calaveras co., *Davy* no. 1390; Yosemite, *Bolander* no. 4820; Fresno, *Buckminster* (type of *N. gracilis*); Kaweah, *Hopping* no. 8; Grapevine spring, Tulare co., *Woolsey*; "California," *Bigelow* (*Whipple expedition*).

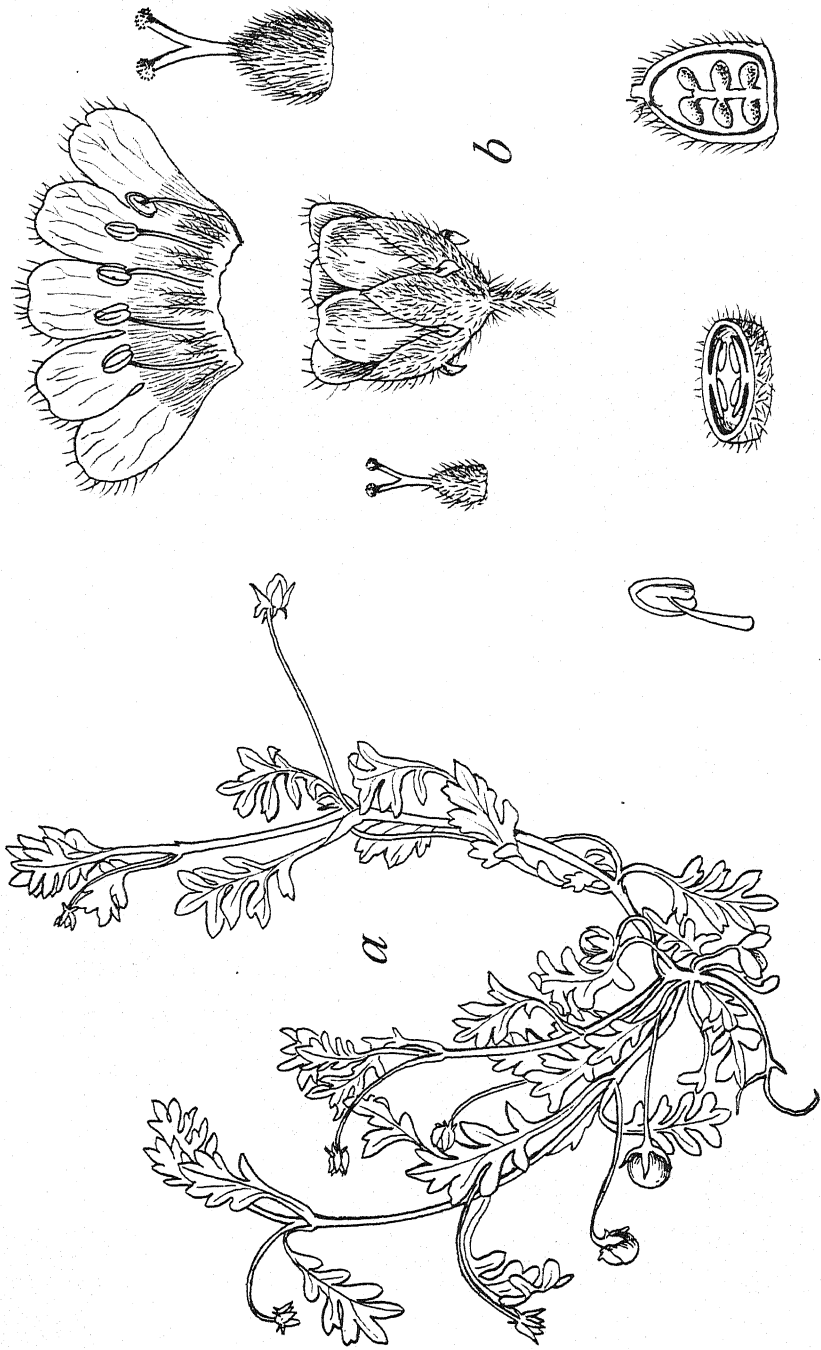
Type in the herbarium of the California Academy of Sciences, San Francisco; collected "on the Hog ranch road, Tuolumne county, California, by J. W. Congdon, June 9, 1897."

18. *N. EXILIS pulchella* (Eastwood) Chandler, comb. nov. — *N. pulchella* Eastwood, Bull. Torr. Bot. Club 28: 157. 1901. — Calyx-lobes linear, extending almost to the base; the appendages very minute or more often entirely wanting: corolla rotate-campanulate, mostly deep blue; scales linear, ciliate.

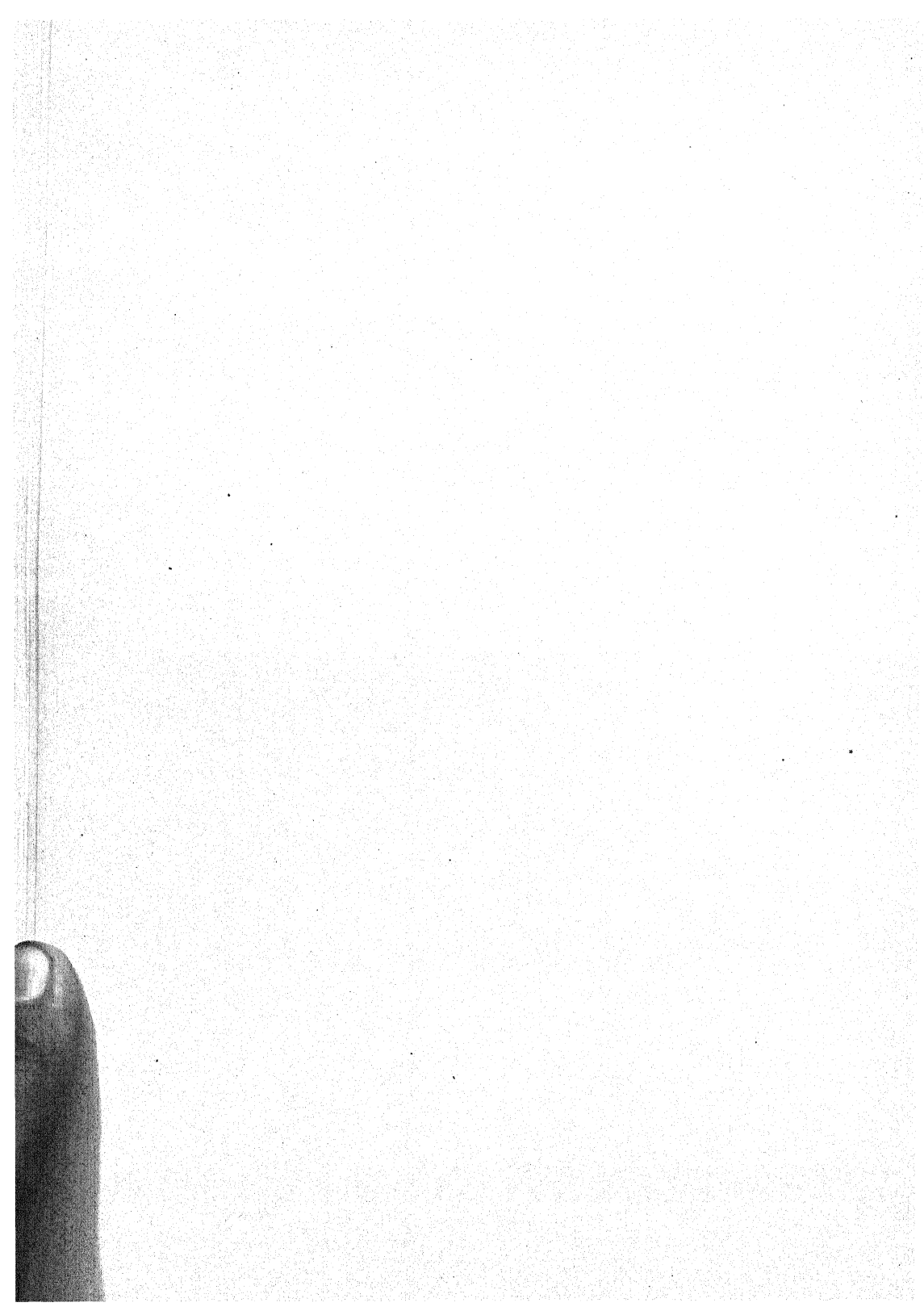


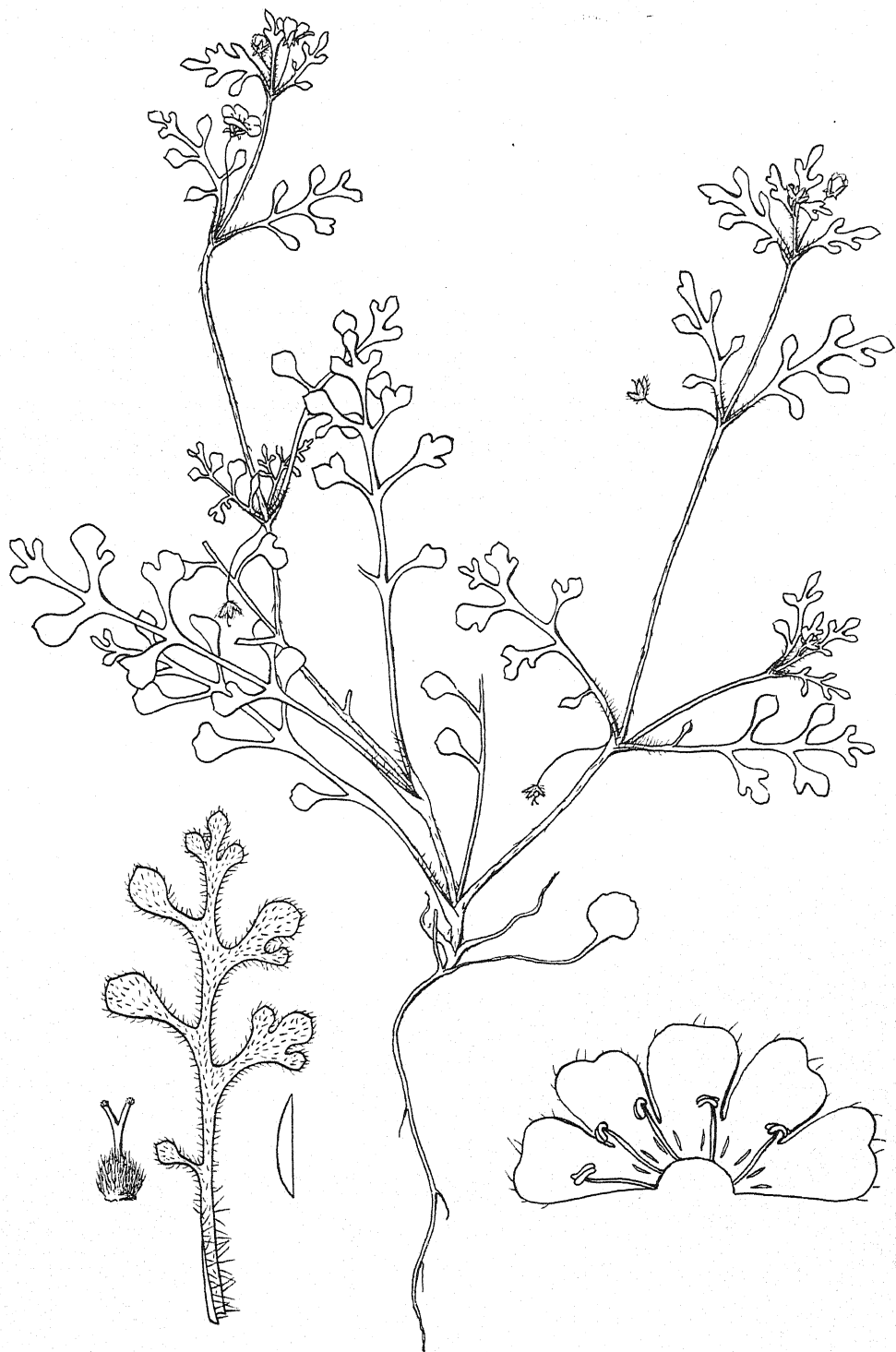
NEMOPHILA SEPULTA Parish



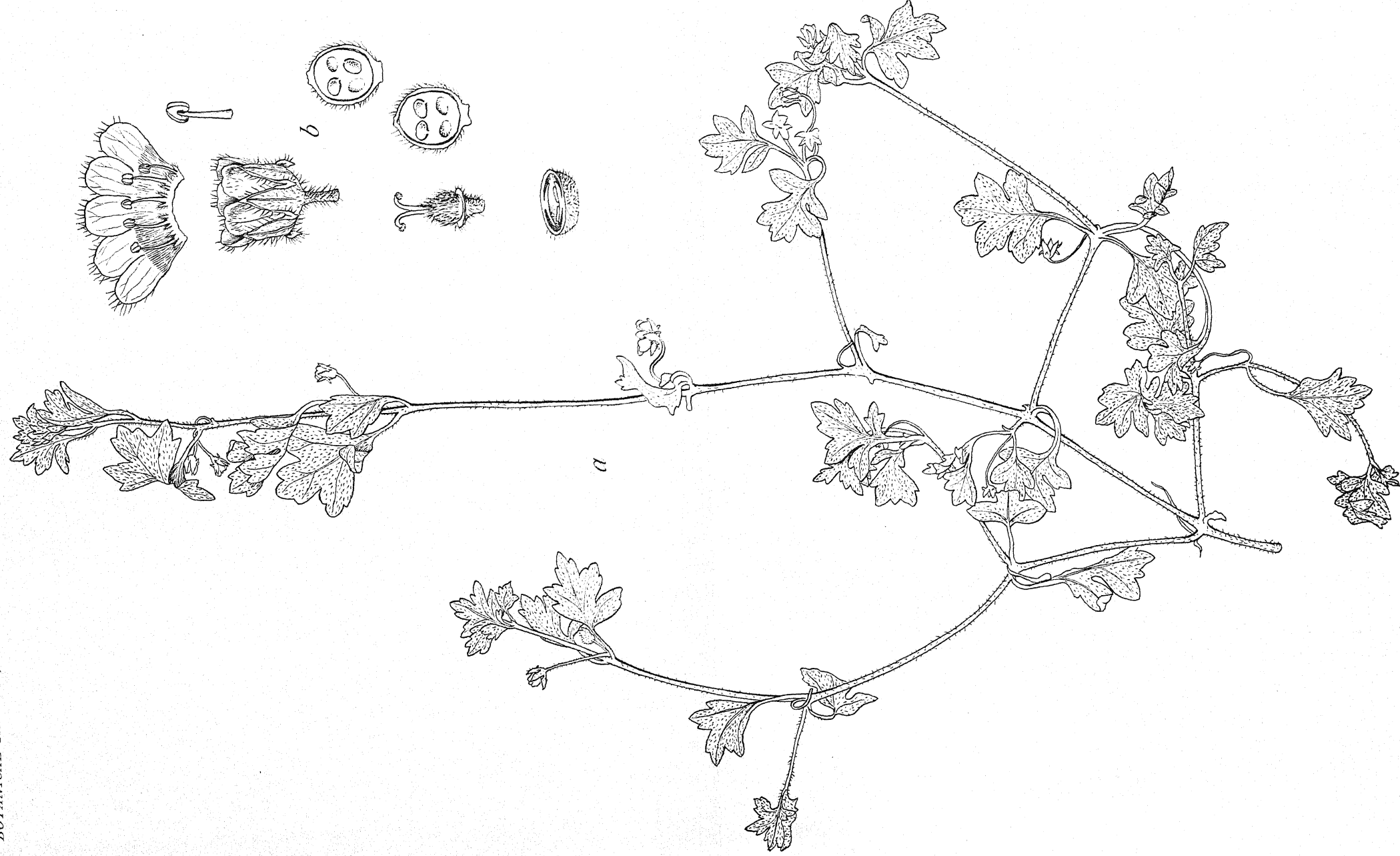


NEMOPHILA PEDUNCULATA Dougl.





NEMOPHILA PARVIFLORA Dougl.



NEMOPHILA EXILIS Eastwood

FOOTHILLS OF THE SOUTHERN SIERRA NEVADA.

Specimens examined: CALIFORNIA: Fresno co., *Eastwood*, *Eisen*; Sequoia park, *Jepson* no. 622; Kaweah, *Hopping* no. 37; Fraser's mill, Tulare co., (?) *Brandeggee*; Salt creek, Tulare co., *Eastwood* (type); Cramer, Tulare co., *Brandeggee*; Bear creek, Tulare co., *Purpus* no. 1720.

Type in the herbarium of the California Academy of Sciences, San Francisco; collected by Alice Eastwood on Salt creek, Tulare county, California.

UNIVERSITY OF CALIFORNIA.

EXPLANATION OF PLATES II-V.

Plate II. Nemophila sepulta Parish.

Specimen from the type locality (Parish no. 4908); natural size.

Plate III. Nemophila pedunculata Dougl.

A. Portion of the type; natural size.

B. Analysis, drawn from a plant collected by Dr. Thomas Coulter in California (no. 480).

Plate IV. Nemophila parviflora Dougl.

A. Type specimen; three-fourths natural size.

B. Analysis, drawn from a specimen in the herbarium at Kew.

Plate V. Nemophila exilis Eastwood.

Specimen from Berkeley, California (typical of the species, of which the type specimen is regarded as an extreme form); natural size.

THE EVOLUTION OF THE VASCULAR TISSUE OF PLANTS.

W. C. WORSDELL.

(WITH SEVEN FIGURES)

It is a sign of the times and of the natural progress which botanical science is making that the evolution of the more deeply seated part of the organization of plants is beginning to receive attention. The most vital and important part of the anatomical structure is doubtless that of the vascular system,

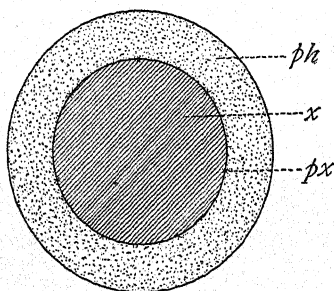


FIG. 1.—The protostele: *x*, xylem; *px*, protoxylem; *ph*, phloem.

and it is the development of this upward through some of the most important groups of plants of which I propose to take a general survey.

We appear to be justified in looking for the primary origin of the complex vascular structure of the stems of cormophytes in the single *solid stele*, the *protostele*, consisting of a central mass of wood, or xylem, surrounded by a zone of bast, or phloem (*fig 1*), this in its turn having been derived from the primitive conductive tissue of the sporophytic stem of some bryophytic ancestor. If we take the great group of the ferns this structure always appears as the first stage in the individual development of each type, as has been shown by the researches of Leclerc du Sablon² and others. This is also the type found in the mature vascular structure of several of the most primitive ferns, such as the Hymenophyllaceae, *Lygodium* (Schizaeaceae), and *Gleichenia*, among modern forms, and *Botryopteris* among fossils.

²SABLON, LECLERC DU, Recherches sur la Tige des Fougères. Ann. Sci. Nat. Bot. VII. 11: —. 1890.

The next stage in general evolution, as the writer holds, is that in which a *pith* arises in the center of the solid stele (fig. 2.), on the outer limit of which an endodermis, or starch-sheath, may or may not be present; this is seen in such forms as *Platy-zoma* (Gleicheniaceae,) *Schizaea*, the *Ophioglossaceae*, and in the fossils *Zygopteris* and *Anachoropteris* (Botryopterideae). The possibility, however, of these forms having been *reduced* from type 3 is not excluded. In all these ferns the protoxylem, or first-formed portion of the wood, is either situated within the metaxylem, or later-formed portion, a short distance from the periphery, or else, as in *Lygodium*, quite at the periphery; that is to say, the xylem is chiefly *centripetal* in its development.

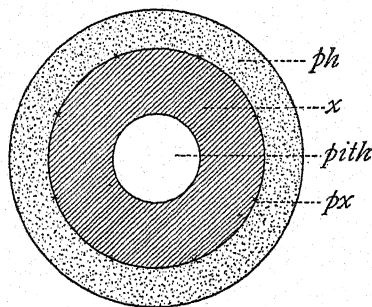


FIG. 2.—The tubular stele with central pith: *x*, *px*, *ph*, as in fig. 1.

The *solenostele* is the name given to the third stage of differentiation, in which to the internal endodermis is added an *internal zone of phloem* (fig. 3.); this is found in *Matonia*, *Loxsona*, *Aneimia Mexicana* (Schizaeaceae), and in a few other plants, such as *Medullosa stellata* among the Cycadofilices.

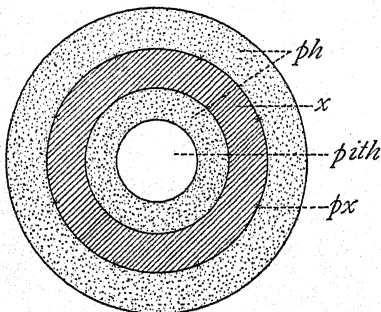


FIG. 3.—The solenostele: reference letters as before.

The *dialystelic* condition appears to have been the next step onward, in which the tubular solenostele becomes split up into a number of secondary solid steles or *concentric strands* (fig. 4), the protoxylem, as in the previous stages, being situated at or near the external limits of the xylem. This structure is directly due to the crowded arrangement of the leaves on the stem, so that frequent gaps in the original solenostele become inevitable in order to allow of the passing out of the leaf-trace

bundles; the whole is thus merely a variant on the solenostele, in which latter the leaf-insertions are not crowded; both conditions belong essentially, as Jeffrey² has admirably shown, to the *siphonostelic*, or tubular type of stele. Van Tieghem³ was therefore in error in regarding the dialystelic condition as derived merely

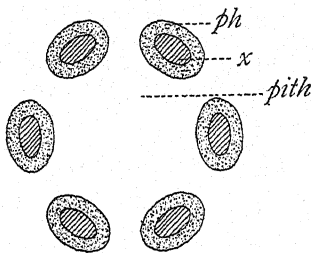


FIG. 4.—The dialystelic condition.

from branching of the primitive solid stele. Dialystely is very common in ferns, occurring in Marattiaceae, *Ancimia Phyllitidis* (Schizaeaceae), Cyatheaceae, Dicksoniae, and in almost all Polypodiaceae, the most advanced of the fern series. The vascular cylinders of *Osmunda regalis* and *O. cinnamomea* probably represent, as Jeffrey⁴ has recently suggested, *reduced* forms, in a greater

and a less degree respectively, of the dialystelic condition. It is also found in several of the Cycadofilices, the group intermediate between ferns and cycads, such as the Medulloseae and Cladoxylon, all fossil types.

If we now take these last named *polystelic* plants as our starting point, we may trace from them the origin and evolution of the vascular tissue of the gymnosperms. The modification which eventually produced this latter consisted, as the writer, along with Potonié,⁵ holds, in the gradual reduction of the concentric type of bundle or stele to form the first and simplest *collateral* type. In a form like *Medullosa anglica* there is a single ring of concentric steles. The theory which the writer regards as best explaining the facts is this: in order that it might give rise to the next succeeding type, as he regards it, represented by such forms as the fossil Cycadofilices, *Lyginodendron* Old-

²JEFFREY, E. C., Trans. Brit. Assoc. Adv. Sci. 869. 1897; Mem. Bost. Soc. Nat. Hist. V. 5: 160.

³VAN TIEGHEM, PH., Sur la Polystélie. Ann. Sci. Nat. Bot. VII. 3: —. 1886; Traité de Botanique, p. 1370. 1892.

⁴JEFFREY, E. C., The structure and development of the stem in pteridophytes and gymnosperms. Phil. Trans. Roy. Soc. June 1902.

⁵POTONIÉ, Lehrbuch Pflanzenpalaeontologie, 1899.

hamium, Poroxylon, and others, each concentric stele composing the cylinder of *Medullosa* underwent a reduction of the tissue on its inner side, whereby the phloem and the whole of the secondary wood of that side vanished, leaving behind what is known as a *mesarch* bundle, consisting of a central or an external protoxylem, with a group of primary metaxylem on both its inner and outer side, or solely in the former region; as a rule, a greater or less development of secondary wood and phloem occurs on the outer side of each bundle. The secondary wood usually extends across the gaps separating the bundles, to form a continuous solid cylinder enclosing a pith, thus tending eminently to obscure the original and primitive condition of a ring

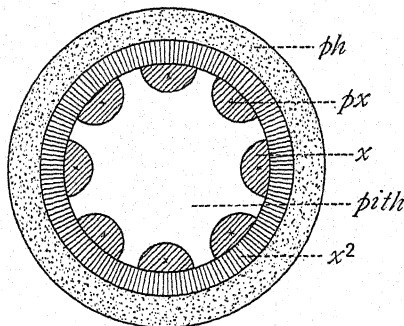


FIG. 5.—The primitive mesarch type: reference letters as before; x^2 , secondary xylem.

of reduced concentric strands (fig. 5). That these latter are each of them really a vestige of a concentric bundle, such as that of *Medullosa*, is shown very well in the case of *Lyginodendron Oldhamium* by the arc- or horseshoe-shaped outline of the bundles, as also by the occasional occurrence of secondary xylem and phloem on the *inner* side of some of the bundles, exhibiting an *inverted orientation*, as if to remind us that the concentric is the original type of structure of these strands. (Dr. D. H. Scott⁶ supposes that the stem cylinder of *Lyginodendron* has been derived from the single solid stele of *Heterangium* (another of the *Cycadofilices* from the Coal-measures), by means of the extinction of the whole of its central solid xylem with the exception of the primary tracheides on the immediate inner side of each protoxylem group. But the writer fails to see much ground for holding this view. The very compact stele of *Heterangium*, with the neatly and evenly circular outline of the inner limits

⁶Scott, D. H., *Studies in fossil botany*, p. 340, 1900.

of the secondary wood, exhibits no sign whatever of having given rise to the more or less distinctly individualized curved bundles of the cylinder of *Lyginodendron Oldhamium*. The writer, on the contrary, believes it to be the homologue of a single stele of *Medullosa*, and can trace a gradual reduction in

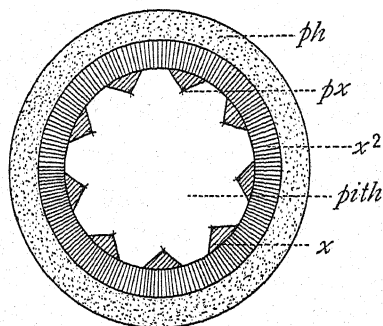


FIG. 6.—The endarch type: reference letters as before.

the number of steles in these plants, from the very numerous ones of *Medullosa Solmsii*, firstly, to the very few steles (two or three in number) of *M. anglica* or *Colpoxylon*, and finally, to the single large stele of *Heterangium* or of *Megaloxylon*. He may add, moreover, that the derivation of the tubular from the solid stele is to be sought for, not in these semi-gymnos-

perous forms, but much farther back, viz., among the ferns.

(When we arrive at the stage of our modern cycads, which are certainly descended from some of these cycadofilicinean plants, a further modification meets our eyes, for here we find the mesarch bundle of the stem cylinder almost entirely replaced by the *endarch* type, in which the innermost primary or centripetal group of xylem has vanished, so that the protoxylem which, once upon a time in the ancient concentric bundle, occupied the center of the latter, now constitutes the most internal portion of the bundle, viz., that nearest the pith (*fig. 6*). But the older mesarch bundle has not become completely extinct throughout the group, for in that most primitive of axial organs, the peduncle of the cone, the centripetal xylem in part persists, as can be well seen in *Stangeria* and *Bowenia*. Those cycads, such as *Cycas*, *Encephalartos*, *Macrozamia*, and *Bowenia*, which possess more than one vascular cylinder in the stem, one within another to the number sometimes of a dozen (a truly striking character), are descended from such types as those *Medulloseae* having more than one cylinder or ring of concentric bundles,

as has been practically proved by the occurrence of obvious vestiges of the concentric type of structure, such as prevails among the Medulloseae, both in the vegetative stems and in the peduncles of all the pluricylindric forms of modern cycads.

In the Coniferae, from the yew tribe upward to the pines, as also in the Gnetaceae, all trace of the primitive mesarch type of bundle has disappeared from the stem, and we find the endarch type, with protoxylem impinging directly on the pith, universally prevailing. That ancient Devonian and Carboniferous plant, *Cordaite*, and our modern maidenhair tree, *Ginkgo biloba*, assumed also, in accordance probably with the exigencies of their arboreal habit, the endarch type of bundles in the stem. But *Pitya antiqua*, *P. primaeva*, *Calamopitys fascicularis*, *C. beinertiana*, and *Dadoxylon Spencersi*, forms perhaps allied to *Cordaite*, still retain the older mesarch type.⁷

As regards the foliar organs of all of these plants we have been considering, it is found that the primitive character of the vascular structure is in them much more persistent than it is in the stem. The concentric fern-type of bundle is still present in the leaf-stalks of *Lyginodendron* (*Rachiopteris*) and *Heterangium*, that of the former plant consisting of a solid stele with three or more protoxylem groups at its periphery, the whole being surrounded by phloem (*fig. 7*). In *Medullosa*, *Cordaite*, and modern cycads the bundles of the leaves are collateral and mesarch in structure; as are also those of the foliage leaves of conifers, although here the centripetal primary xylem is either greatly reduced or modified to form a quasi-new structure, the *transfusion tissue*. In *Ginkgo* this reduction also obtains in the foliage leaf. But in the most primitive vegetative foliar organs of the plant, the cotyledons, both in *Ginkgo* and *Cephalotaxus* (the

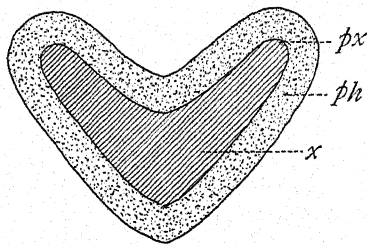


FIG. 7.—Concentric bundle of leaf-stalks.

⁷SCOTT, D. H., On the primary structure of certain palaeozoic stems with the *Dadoxylon* type of wood. Trans. Roy. Soc. Edinburgh 40: [pt. II]. 1902.

most ancient of the conifer group), the mesarch structure of the bundle is as pronounced and well developed as it is in the case of the cycads or Medulloseae. As regards these two latter groups, the writer regards their mesarch bundles as derived from the splitting up of one or more concentric bundles like that of *Lyginodendron*. In any case the mesarch collateral bundles of the foliar organs of all these plants are to be regarded, like those of the stem, as reductions from the concentric type. But this concentric type actually occurs here and there in the sporophylls of the cycads.

On arriving at the level of the angiospermous plants, all trace of any vestige of the old concentric type of bundle in the form of a mesarch structure has completely vanished both in the stem and in the leaf, the purely endarch structure prevailing everywhere. The fact of this type of structure occurring well-nigh universally in these plants which, in other parts of their organization, are seen to be the most advanced in evolution of all plants, is an indication that this type of vascular structure is also to be regarded as the most advanced, because the most advantageous and the best adapted to the requirements of the plants exhibiting it. The writer, however, considers that the conclusions drawn by Jeffrey, from the study of the vascular cryptogams, as to the origin of the vascular tissue of the stem are rather too hastily applied to the case of the angiosperms. We are not yet in a position to say whence the vascular system of these latter plants was derived. All we dare surmise is that, looking far enough back, it is probable that the vascular tissue of the angiosperms had an origin similar to that of the forms below them in the scale.

The cause of the disappearance of the primitive mesarch structure can be seen in tracing the evolution of the vascular tissue from such forms as the Medulloseae upward. Obviously, the most economical method of increasing the amount of vascular tissue for purposes both of conduction of water and food substances and of resistance to bending strains would be by the addition, through the means of a cambium, of new tissue on the *outer circumference* of the stele or cylinder; now, in pro-

portion as the tissue in this region increased in thickness, there took place, correlatively therewith (what, indeed, would be, *a priori*, obviously expected) a gradual reduction of the centripetal vascular tissue, viz., that on the medullary side of the protoxylem, whether secondary or primary. This can be seen beautifully exhibited within the Medulloseae group itself, eventually culminating in the stem structure of modern cycads. The process of elimination of the centripetal xylem proceeded apace, until finally the endarch stem structure of Cycads, Coniferae, Cordaites, Gnetaceae, and Dicotyledons, as being by far the most economical and advantageous method of vascular formation, eventually prevailed.

In the case of leaves there has not been such a demand for modification of the vascular tissues as was the case with the stem, hence the longer persistence of the older character in these organs.

In roots the primitive centripetal structure of the wood has been far more persistent, probably for the purpose of enabling these organs to resist central tension strains.

In Monocotyledons, although true secondary thickening does not occur, the endarch type of bundle nevertheless obtains; where the concentric structure is found, as in those cases of bundles with a central phloem, this is merely to be regarded as a modification of the endarch type.

KEW, SURREY, ENGLAND.

BRIEFER ARTICLES.

SUGGESTIONS ON THE CLASSIFICATION OF SEEDS.

MODERN botanical text-books do not present a classification of seeds in accordance with modern ideas of their structure and function. It comes as a distinct surprise to the average student of plants when he, for the first time, appreciates that some familiar herb, shrub, or tree may bear during a single season a score or more different types of seeds. Nor does the great complexity underlying the concept of the seed seem to be fully comprehended by the plant breeders and seed growers. Indeed, no method has been devised for recognizing the types of seeds that theoretically exist, nor, so far as I am informed, has a nomenclature been provided by which one type may be delimited from another. Under these circumstances it seems desirable to set down a simple classification of the more fundamental types of seeds in the hope that future experiment will indicate marks by which they may be recognized, and that some new light may thus be thrown upon the problems of hybridization, seed control, variation, mutation, and evolution of varieties and species.

To define the word "seed" in a manner technically accurate is exceedingly difficult. Underneath the seed lie the following conditions, in the absence of any of which the seed does not exist as such:

1. Alternation of generations. No seed is ever produced by non-alternating types of plants.
2. Heterospory. Among alternating types seeds are not produced by homosporous forms.
3. Intraspecific symbiose. Heterosporous types devoid of intergenerational symbiosis do not produce seeds.

The seed is in no exact sense an organ of the plant that bears it; it is rather an aggregate in the family life of the species. In its tissues and structures belonging to three consecutive generations are uniformly present either transitorily or permanently. While its significance for the persistence of the species may be very great, it cannot be

regarded as a reproductive organ in the sense in which an antheridium, archegonium, or sporangium is so regarded.

A common definition of the seed describes it as a "ripened ovule." The full value of this is appreciated when one finds the ovule defined as an "immature seed." Seeds, however, occur in plants destitute of ovules, in the ordinary sense, and in any event a thorough definition is desirable. The following statement covers, to some degree, the modern concept of the seed: "A seed is an ultimate, trigenerational, symbiotic unit in the plant life-history, integrated from tissues and structures belonging to two sporophytic generations and the intervening gametophytic phase." By a somewhat vague and imperfect analogy the seed might be compared with the "household" in human society. Like the average household it comprises organisms linked by consanguinity and consecutive in development.

Thus defined, seeds may be classified into the following groups, the significance of which is essentially phylogenetic.

I. GENERAL CLASSIFICATION.

Seeds facultative.

Example, *Selaginella*.

A. Pseudosperms.

Seeds obligatory.

B. Eusperms.

1. Embryos monomorphous.

a. Pteridophytic seeds.

I. Pteridosperms.

Example, *Lepidostrobus*.

b. Archespermic seeds.

II. Archesperms.

2. Embryos dimorphous.

a. Metaspermic seeds,

III. Metasperms.

In the above it will be observed that the basis for the separation of seeds into the two fundamental groups is determined by their appearance as (1) unnecessary or (2) necessary aggregates in the life of the species. In by far the great majority of seed-bearing plants seeds are characteristic and are normally developed as such. In *Selaginella* certain megasporangia have been observed to remain for a long time indehiscent, and in this condition, their spores having germinated, and the eggs having been fecundated, to assume the character of seeds. This is, however, not the rule in the genus but the exception, hence such seeds have here been named facultative seeds or Pseudosperms, to distinguish them from the obligatory seeds or Eusperms of plants in which indehiscence of the megasporangium has become the rule, and the seed is thus fixed as a normal unit in the life-history.

It will also be observed in the limitations of the classes of Eusperms that the double fecundation of Nawaschin and Guignard is accepted as a true fecundation. This position is capable of defense, but even if later proved untenable the two classes of Archesperms and Metasperms are sufficiently distinct to justify the nomenclature.

II. STRUCTURAL CLASSIFICATION.

Seeds integrated with placenta.

(Inseminées of Van Tieghem,¹ *e. g.*, Loranthaceae.)

Seed integrated separately from placenta.

(Seminées of Van Tieghem.)

A. Synsperms.

B. Aposperms.

Under the head of structural classification should be mentioned also the division of seeds into monocotyledonous and dicotyledonous according to the character of the embryo, into albuminous and exalbuminous, according to the persistence of the endosperm, into ategminées, unitegminées, and bitegminées (Van Tieghem), according to the presence and number of the integuments, etc., but these classes are after all of comparatively secondary importance. They do not bring into view fundamental differences between seeds, but only incidental. For example, the difference between the monocotyledonous and the dicotyledonous embryo is probably by no means of fundamental importance, but represents different adaptations of haustorial organs during intraseminal life; the difference between albuminous and exalbuminous seeds arises through nutritive adaptations between embryo and endosperm and is of secondary importance; the difference between seeds with one or two integuments is after all a question of indusial development and need not be given great weight. It is true that these distinctions are of great value to the taxonomist and enable him to classify plants to advantage. Yet in comparison with the distinctions brought out below they are probably less significant in the specific life.

¹ The classification of flowering plants constructed by Van Tieghem principally upon the basis of seed structure contains much of interest. Unfortunately it is not natural, the characters taken for primitive being in many instances either vestigial or derived. Thus it results in an inversion of relationships. This is well illustrated by the position given to such a family as the Loranthaceae. On account of the high ecological specialism of the plants herein included degenerate structures would be certain to appear. It is precisely these that Van Tieghem accepts as primitive. This fact in itself is perhaps a sufficient commentary on the taxonomic value of the Van Tieghem sequences.

III. GENETIC CLASSIFICATION OF METASPERMS.

A. Seeds with parthenogenetic embryos.

A. Parthenosperm.

I. Both embryo and endosperm parthenogenetic.

I. Euparthenosperm (1)

II. One plant, either embryo or endosperm, not parthenogenetic.

II. Hemiparthenosperm

a. Endosperm result of fecundation, embryo parthenogenetic

a. Parthenembryosperm

1. Effective pollen arising in same flower with seed.

1. Autembryosperm (2)

2. Effective pollen arising in neighboring flower on same stock.

2. Geitonembryosperm (3)

3. Effective pollen arising in flower of another stock.

3. Xenembryosperm (4)

4. Effective pollen arising upon stock of another species or variety.

4. Bastardembryosperm (5)

b. Embryo the result of fecundation, endosperm parthenogenetic.

b. Parthenendosperm

1. Effective pollen arising in same flower with seed.

1. Autendosperm (6)

2. Effective pollen arising in neighboring flower on same stock.

2. Geitonendosperm (7)

3. Effective pollen arising in flower of another stock.

3. Xenendosperm (8)

4. Effective pollen arising upon stock of another species.

4. Bastardendosperm (9)

B. Seeds with no parthenogenetic embryos.

B. Gamosperm

a. Embryos arising through autogamy.

a. Autosperm (10)

b. Embryos arising through allogamy.

b. Allosperm

1. Embryos arising through geitonogamy.

1. Geitonosperm (11)

2. Embryos arising through xenogamy.

2. Xenosperm (12)

c. Embryos hybrid.

c. Bastardosperm (13)

The figures 1-13 following the names designate fundamental seed types all of which theoretically might arise upon a single plant. Naturally, however, seeds of one or two types will be produced in abundance by the individuals of a species, while others will be extremely

rare. In the genus *Viola*, for example, plants with cleistogamous flowers will normally produce both autosperms and xenosperms. In *Polygala*, species exist capable, from the ecological relations of their flowers, of producing a greater variety of seeds. These would differ essentially in their manner of development, while resembling each other structurally to such a degree that they would be indistinguishable by any of the ordinary tests. Furthermore, it may very well be that the xenosperm borne on a stock which is itself the development from a xenosperm will differ intrinsically from the xenosperm which is borne upon a geitonospermous or autospermous stock. Thus a new element of complexity is brought in and an explanation is perhaps afforded of so-called "sports" or mutations. Here also may be an explanation of certain genera which include large numbers of closely related "species." May it not be possible that in a species there will be distinctive xenosperm, autosperm, geitonosperm, and parthenosperm varieties, the continual production of which gives an appearance of *related species* rather than of special seed varieties? For example, would this explain *Crataegus*, *Rubus*, and *Hieracium*? And may not the mutation forms of *De Vries* be plants which have arisen from rare and unusual seed-types, developed, however, in accordance with the laws of plant reproduction?

In any event the consideration of the regular causes that underlie the observed individuality of seeds may lead to useful results in plant-breeding. It seems very certain that to regard seeds as necessarily equivalent because borne upon the same stock is a grave and positive error. They may even pass all the ordinary tests and yet be extremely unlike, so much so that they will upon development give rise to plants so different that they may rightly be classed as different species. Returning to the analogy mentioned above, it would seem as if there were no more reason to deny individuality to the seeds borne in a head of grain, upon *prima facie* evidence, than there would be to deny the individual character of each household in a city.

—CONWAY MACMILLAN, *University of Minnesota*.

THE SENSITIVE PLANT AS A WEED IN THE TROPICS.

(WITH ONE FIGURE)

EVERYONE who has traveled much in the tropics knows that *Mimosa pudica* is a weed which gives considerable trouble to the

planters, but so far as I am aware no photographs of the way it luxuriates have been published. It may be interesting to those who have not seen the plant in its own home to look at a photographic reproduction of a large patch of it which I observed recently in Ceylon.

I was returning from Peradeniya to Colombo and the train stopped for a few minutes at a way station in the lowlands, an hour's ride from the city, just long enough, in fact, to allow me to get a snap-shot.



Mimosa pudica, as it grows luxuriantly in Ceylon.

of a field quite disfigured by Mimosa. The cattle pastured in the field had eaten the herbage closely around the plant, leaving it strictly alone, and as it crept across the meadow it killed out all other plants, forming a dense deep patch of spiny, creeping stems and delicate pink blossoms, which resembled miniature dandelion or thistle heads gone to seed.

The leaves were all expanded horizontally as I approached, but when my feet shook the soft earth, like a hermit crab draws into its shell, or a coral pulls in its tentacles, the plants, in the radius of the shaken ground, quickly folded their leaflets together and dropped their leaves into the characteristic position of rest which everyone knows who has seen the living plant.

To one acquainted only with the delicate specimens in European and American greenhouses, the novelty of walking over such beds of

it in the tropics does not soon wear off. I have been on railway lines whose embankments were covered with *Mimosa*, and watched with keen amusement, as the train advanced, the quick falling of the leaves like the progress of a roller on the seacoast.

In Ceylon the planters complain that it is among their most troublesome weeds, and one sees it everywhere in the cocoanut groves and tea plantations. Though highly interesting and valuable in a botanical laboratory, *Mimosa pudica* is quite useless on a tropical estate.—DAVID G. FAIRCHILD, *U. S. Department of Agriculture*.

CURRENT LITERATURE.

MINOR NOTICES.

THE TENTH PART of Wiesner's *Die Rohstoffe des Pflanzenreiches*¹ concludes the twenty-first section (641-684) on *Blüthen und Blüthentheile*, contains the twenty-second section (685-781) on *Samen*, and begins the twenty-third section on *Früchte*.—J. M. C.

"THE MOSSES OF ALASKA"² is the title of the 29th paper from the Harriman Alaska Expedition, and J. Cardot and I. Theriot are the authors. Not only are the mosses collected by the Harriman Expedition of 1899 included, but also species previously reported from the region. The whole number enumerated is 280, of which 124 are new to Alaska, and 46 new to science. The 26 new species are distributed among the following genera: *Cynodonium*, *Dicranum*, *Trichostomum* (2), *Barbula* (4), *Rhacomitrium*, *Ulota*, *Orthotrichum*, *Entosthodon*, *Webera*, *Bryum* (8), *Polytrichum*, *Brachythecium*, *Plagiothecium*, and *Hypnum* (2).—J. M. C.

IN A STUDY of the conditions influencing the germination of the spores of *Agaricus campestris*, Miss Margaret C. Ferguson³ has found "that if a few spores are able to germinate under the cultural conditions, or if a bit of the mycelium of *A. campestris* be introduced into the culture, the growth resulting will in either case cause or make possible the germination of nearly all the spores of the culture, provided, of course, that the other conditions are not such as to inhibit germination." Cultures in various substances and under different conditions showed much variation in germination but no very constant results. The article is accompanied by three plates, illustrating the growth of *A. campestris* and culture methods employed.—R. E. SMITH.

THE THIRTEENTH (1902) report of the Missouri Botanical Garden consists chiefly of a paper by Dr. Trelease, entitled "The Yuccae" (pp. 27-133, pls. 100). The four genera are *Hesperaloe*, with two species; *Hesperoyucca*, regarded as a monotypic genus; *Clistoyucca*, a subgenus of Engelman's raised to generic rank and containing one species; *Yucca*, with

¹ WIESNER, JULIUS, *Die Rohstoffe des Pflanzenreiches*, etc. Volume II, pp. 641-800. figs. 200-248. Leipzig: Wilhelm Engelmann. 1902. M 5.

² Proc. Wash. Acad. Sci. 4: 293-372. pls. 13-23. 1902.

³ A preliminary study of the germination of the spores of *Agaricus campestris* and other basidiomycetous fungi. Bull. 16. Bureau Plant Industry, U. S. Dept. of Agric. pp. 43. pls. 1-3. 1902.

twenty-eight species, six of which are new; and *Samuela*, a new genus comprising two species. Detailed synonymy, descriptions of numerous varieties, and full discussions of relationships are presented. The plates for the most part are reproductions of excellent photographs, showing habit and certain details; three plates are devoted to seeds, and twelve to geographic distribution.—J. M. C.

VERSCHAFFELT⁴ has studied the occurrence of hydrocyanic acid in developing shoots of *Prunus Padus* and *P. Laurocerasus*, with the following results: As the buds open and the shoot develops, the HCN-compounds increase in amount as rapidly as do the other substances, so that the percentage amount of these compounds changes very little. It seems that these hydrocyanic bodies appear independently of light, and that they are not derived from the internode below the growing bud. In what form the hydrocyanic acid occurs is not yet determined. That maceration is necessary before complete distillation of the acid can occur would seem to indicate the presence of some compounds which can be split by an enzyme. The marked occurrence of benzaldehyde in the distillate from the developing buds makes it probable that glucosides related to amygdalin are present.—B. E. LIVINGSTON.

A RECENT BULLETIN of the U. S. Department of Agriculture, Bureau of Soils, contains three valuable papers by Briggs and Lapham⁵ on soil physics. Following are some of the conclusions: (1) dissolved salts in general do not increase the capillary rise of soil waters; (2) concentrated solutions of all salts materially decrease capillary activity, but this effect is less marked with sodium carbonate than with natural salts; (3) the capillary rise of water in moist soil is much greater than in soil which was air-dry at the beginning of the experiment; thus for sea-island soil it was found that the maximum rise in dry soil was 37^{cm}, while the limiting value of capillary movement in moist soil was not less than 165^{cm}; (4) suspended clay may be advantageously separated from soil solutions by means of a porous clay filter tube and a compressing air pump, the solution being forced through the filter by increased air pressure.—B. E. LIVINGSTON.

A NEW SERIAL PUBLICATION has appeared, entitled *University of California Publications, Botany*, and intended to be a series of original papers in botany. Each volume will contain about 350 or 400 pages, and the subscription price is \$3.50, the papers comprising those on general botany and West Coast botany. Professor W. A. Setchell is the editor of the series.

⁴VERSCHAFFELT, E., On the prussic acid in the opening buds of *Prunus*. Koninkl. Akad. van Wetenschap. te Amsterdam. 31-41. (Je 25) 1902.

⁵BRIGGS, L. J. and LAPHAM, M. H., Capillary studies and filtration of clay from soil solutions. Bull. 19. Bureau of Soils, U. S. Dept. of Agric. 1902.

The first number is a paper by Harvey Monroe Hall,⁶ entitled "A botanical survey of San Jacinto mountain". The general features of the mountain as to position, topography, soil, climate, and geology are given. This is followed by an account of the plant distribution, both on the basis of life zones and phytogeographic formations. The latter are presented as chaparral, forests, undergrowth, meadows, riparian formation, pond formation, and crest formation. The factors affecting plant distribution are discussed under the heads of altitude, temperature, moisture, slope exposure, desert winds, rock surface, avalanches, land slides, and water courses. The flora is said to be composed of distinct boreal and austral elements, with an admixture of certain Arizonan and New Mexican species. A catalogue of the species collected in or above the yellow pine belt includes 9 gymnosperms, 78 monocotyledons, and 365 dictotyledons. New species are described in *Elymus*, *Stipa*, *Oxytheca*, *Potentilla* (2), and *Erigeron*.—J. M. C.

F. HEYDRICH⁷ has presented a novel theory as to the homology of the tetrasporangium in the Rhodophyceae. This structure he regards as the predecessor of the cystocarp and hence a true sporophyte. The idea is at least a suggestive one, but its establishment would require a far more careful and thorough investigation than the author apparently has made. He bases his work on Oltmann's studies, where it has been shown that the fertilized nucleus of the carpogonium passes out into the auxiliary cell and there by division gives rise to the spores. This nucleus, however, never undergoes a secondary fusion with the auxiliary nucleus. Heydrich finds that two cells are concerned with the production of the tetrasporangium. These cells arise from a pericentral cell of a branch, homologous with the cell and branch from which the procarp arises. The nucleus of the cell nearest the parent branch, the stalk cell, he considers as the fertile energid. This nucleus now divides' one daughter nucleus remaining in the stalk cell, the other passing to the distal cell, which is now the tetrasporangium mother cell. No nuclear fusion takes place, but instead the original nucleus breaks down, possibly contributing somewhat in the way of food to the immigrant. The spores all arise from the entering nucleus. This is a striking parallel with the behavior of the fertilized nucleus of the carpogonium as reported by Oltmann and others.

The examination embraces quite a wide range of forms, including representatives of both the zonate and tripartite types of division, in all of which these conditions are true. Lack of detail in the figures, brief treatment of many important stages, homologizing structures, in some cases on external appearance alone, together with dogmatic statements as to the kinship of nuclei when no mitotic figures are shown, fail to carry the conviction that this

⁶ Univ. Calif. Publ. Bot. 1: 1-140. pls. 1-14. 1902.

⁷ Das Tetrasporangium der Florideen ein Vorläufer der sexuellen Fortpflanzung. Bibliotheca Botanica 57.

theory is to be regarded as firmly established on fact. However, it deserves investigation.—J. J. WOLFE.

THE MITOSES in the megaspore mother cell of several liliaceous forms, especially *Galtonia candicans*, *Scilla sibirica*, and *Tulipa Gesneriana*, are described in great detail in a paper by Schniewind-Thies.⁸ In *Galtonia* the mother cell usually gives rise to a row of four potential megaspores, but occasionally only two cells appear in the row, one of which may germinate directly to form the embryo sac, a transition between the condition in *Lilium*, where the megaspore mother cell develops directly into the embryo sac, and the condition where one of four megaspores produces the sac. In any case, the first mitosis in the megaspore mother cell shows the reduced number of chromosomes. The second division in a form like *Lilium* corresponds in all essential details with the second division in a form which is to have two or four megaspores, and there is a similar correspondence in the third divisions. In *Scilla* it is interesting to note that while the number of chromosomes in the gametophyte is eight, the number in the sporophyte varies from eight to sixteen. In *Tulipa*, at the first mitosis in the mother cell, each of the daughter nuclei contains twelve chromosomes, and in the two succeeding mitoses this number is maintained at the micropylar end of the sac; but at the chalazal end the sporophyte number may appear at the second division, or the number may vary, fifteen, sixteen, and twenty-one having been counted. The writer believes that the new generation begins with the reduction division, both in the embryo sac mother cell and in the pollen mother cell, and he has no doubt that the processes in the ovule and in the microsporangium of angiosperms are homologous. The four potential megaspores correspond to the four microspores (pollen grains); cases of two potential megaspores show a step toward the further reduction which is found in forms like *Lilium*. The fact that the megaspores take the form of a row is due to position, there being no opportunity for early isolation and rounding off as in microsporangia.—CHARLES J. CHAMBERLAIN.

NOTES FOR STUDENTS.

FRANCIS E. LLOYD⁹ has described vivipary in *Podocarpus Makoyi*. The embryo develops continuously, the hypocotyl passing out through the micropyle while the seed is still attached. The phenomenon is said to be well known in Japan, but does not seem to have been recorded in English.—J. M. C.

⁸Die Reduction der Chromosomenzahl und die ihr folgenden Kerntheilungen in den Embryosackmutterzellen der Angiospermen. 8vo. pp. 34. pls. 5. Jena: Gustav Fischer. 1901.

⁹*Rhodora* 2: 113-117. figs. 3. 1902.

F. PÉCHOUTRE¹⁰ has made an extended study of the development of the ovule and seed of the Rosaceae. He describes in detail the formation of the ovular protuberance and the integuments. He finds remarkable uniformity in the development of the sporogenous tissue, a large number of species, representing all regions of the family, showing the many-celled archesporium and general characters of the classic *Rosa livida*. The early stages in the development of the embryo were studied in numerous forms, special stress being laid upon the various phases of the suspensor. All gradations are shown from the small, more or less elongated filamentous form to the short and compact massive type.—J. M. C.

IN LIEFERUNG 213 of Engler and Prantl's *Natürlichen Pflanzenfamilien*, Potonié discusses the Cycadofilices. He notes that this alliance, originally set up in his *Pflanzenpalaeontologie* (1898), has been adopted by Dr. Scott in his *Studies in Fossil Botany*, and by Mr. Seward in the arrangement of the vegetable fossils in the British Museum. Anatomical characteristics make it very probable that the forms included under the heading Cycadofilices are intermediate between the ferns and gymnosperms, although practically nothing is yet known of their reproductive organs. The illustrations, where they are not original, are largely reproductions of the admirably clear figures in Dr. Scott's recent text-book of palaeobotany.—E. C. JEFFREY.

M. L. LUTZ¹¹ shows by cultures that certain algae and fungi are able to absorb and apparently to assimilate amides without first breaking them down into ammonium salts. His experiments were performed upon *Pleurococcus miniatus* and *Raphidium polymorphum* for algae, and upon *Pencillium glaucum* for fungi. A number of amides were tested. The results are in general in accord with those of Czapek¹² in the same field, a fact to which the author calls attention in a note. The only point of disagreement between the two series of cultures independently made by these two authors is in regard to the effect of butyramide upon *Aspergillus*. Czapek failed to obtain growth in this substance; while Lutz records an excellent development therein.—B. E. LIVINGSTON.

THE EFFECT of dissolved oxygen and carbon dioxid upon the development of plankton has been investigated by Whipple and Parker.¹³ The phys-

¹⁰ Contribution à l'étude du développement l'ovule et de la graine des Rosacées. Ann. Sci. Nat. Bot. VIII. 16: 1-158. figs. 166. 1902.

¹¹ Recherches sur la nutrition des Thallophytes à l'aide des amides. Bull. Soc. Bot. France 48: 325-334. 1902.

¹² Zur Kenntniss der Stickstoffversorgung und Eiweissbildung bei *Aspergillus niger*. Ber. Deut. Bot. Gesells. 130-139. 1901. Also, Untersuchungen über die Stickstoffgeweinung und Eiweissbildung der Pflanzen. Hofmeister's Beiträge 1: 538-560. 1902.

¹³ WHIPPLE, G. C. and PARKER, H. N., On the amount of oxygen and carbonic acid dissolved in natural waters and the effect of these gases upon the occurrence of microscopic organisms. Trans. Amer. Micr. Soc. 23: 103-144. pls. 19-22. 1901.

ical principles underlying solution of these gases and the methods best adapted to their determination in natural waters are quite fully treated. Ordinarily both carbon dioxide and oxygen are necessary for the life of the micro-organisms in natural waters. Consideration of the relative amounts of these gases is shown to be of great value in explaining certain problems of vertical and seasonal distribution. What seems to be a causal relation is pointed out between the great carbon dioxide content of ground waters and their peculiar tendency to support diatom growth. Interesting curves and tables accompany the paper.—B. E. LIVINGSTON.

JOHN CUTLER TORREY,¹⁴ in studying the "Cytological changes accompanying the secretion of diastase," concludes that among the grasses "diastase of secretion" arises in the nucleus of the epidermal cells of the scutellum; that zymogenesis begins in the nuclei before the advent of the resting period; that at some time during the first and third days of germination the diastase-secreting cells swell to three or four times their original size; that during the first and third days there are "waves" of secretion, so that this process may be described as intermittent, but from that time on, until final exhaustion of the cells, the secretion is more continuous; that the secreting cells begin to degenerate about the tenth day; that it is highly probable that the chromatin takes an active part in the zymogenesis; that the nucleus is in this case very clearly the metabolic center of the cell; and that there is a marked difference in secretory processes in plants and animals.—J. M. C.

L. COCKAYNE¹⁵ continues the account of his studies of the seedlings of New Zealand and Chatham island plants. He finds that many species common to New Zealand and Chatham islands are similar in their young stages, but become different in their adult forms, the New Zealand forms becoming strongly xerophilous in structure, while those from Chatham island retain their juvenile characters. A number of New Zealand species pass through three distinct stages in their individual development: first the juvenile form, then this gives place to an extremely xerophilous form, and finally this is replaced by a form which resembles the first. Similar forms from Chatham island do not pass through the xerophilous stage, and the New Zealand plants when grown under favorable conditions of moisture omit this stage also, resembling the juvenile form throughout. The author considers the bearing of these facts on the relationships and history of the flora of these two regions.—W. B. MCCALLUM.

VALUABLE DETERMINATIONS of the constituents of the fruit of the coconut (*Cocos nucifera*) are given by J. E. Kirkwood and W. J. Gies.¹⁶ The milk

¹⁴ Bull. Torr. Bot. Club 29: 421-435. 1902.

¹⁵ An inquiry into the seedling forms of New Zealand phanerogams and their development. Trans. New Zealand Inst. 33: 265-299. pls. 10-12. 1900.

¹⁶ Chemical studies of the coconut with some notes on the changes during germination. Contrib. N. Y. Bot. Garden no. 26. Bull. Torr. Bot. Club 20: 321-359. pl. 19. figs. 1-6. 1902.

of the green nut is an aqueous solution containing large proportions of a reducing sugar (probably a mixture of dextrose and galactose) and some cane sugar, together with much hydrochloric and phosphoric acid in combination with both alkaline and earthy bases. There is very little proteid in either milk or endosperm. In the mature nut the milk contains little monosaccharide and much cane sugar. The mature endosperm contains much fat and insoluble carbohydrate material. The fat is mainly glycerides of caprylic, lauric, myristic, and palmitic acids. Besides cellulose, a polysaccharide gum is present in considerable quantity, and several sugars, but these only in small amount. The proteid present is largely edestin. A diastatic enzyme and oxydase occur in both milk and endosperm, but no appreciable quantities of any protoelytic or adipolytic enzyme were found.—B. E. LIVINGSTON.

MISS ETHEL SARGANT¹⁷ has long been studying the vascular system in monocotyledonous seedlings, and has reached the conclusion that the symmetry and structure of the vascular system of the seedling can be used as a guide to the phylogeny of the Liliaceae. She regards the genus *Anemarrhena* as a primitive type in the family, two opposed collateral bundles occurring in the cotyledon. This is taken to represent the "bicotyledonary" system of a remote ancestor. In other words, the monocotyledons are specialized, reduced forms of dicotyledons, in which two separate cotyledons have gradually united. It will be recalled that Mr. H. L. Lyon¹⁸ has suggested on the other hand, that the dicotyledonous condition has been derived from the gradual splitting of the single cotyledon of monocotyledons. Miss Sargent calls attention to the fact that among monocotyledons the apex of the cotyledon often remains within the endosperm, a habit that "would naturally lead in course of time to the fusion of the cotyledons within the seed." In a later number of the same journal¹⁹ Mr. A. G. Tansley objects to this "reduction" theory.—J. M. C.

GEORGE JAMES PEIRCE²⁰ has studied "The root-tubercles of bur clover (*Medicago denticulata* Willd.) and of some other leguminous plants." His conclusions are that though the bacteria that form the tubercles are usually only slowly motile in artificial cultures, this proves nothing as to their motility in the soil: that the proportion of root hairs affected is very small; that infection of the roots may be resisted by cutting off the infected ends of the root hairs; that the bacteria enter a root hair by softening or dissolving a small portion of the wall and moving or growing through this; that the infection thread is chemotropically attracted to the layer of cells next the central cylinder; that the tubercles originate only endogenously and from the same

¹⁷ The origin of the seed-leaf in Monocotyledons. *New Phytol.* 1: 107-113. 1902.

¹⁸ *Minn. Bot. Studies* 643-655. 1901. ¹⁹ *New Phytol.* 1: 131-133. 1902.

²⁰ *Proc. Calif. Acad. Sci.* III. Bot. 2: 295-328. *pl.* 29. 1902.

layer that gives rise to lateral roots, and hence are morphologically lateral roots; that tubercles are largest and most numerous near the surface of the soil; that the presence of bacteria prevents the infected cells from forming starch grains; that the bacteria cause the degeneration and almost complete destruction of the nuclei; that infected cells soon lose the power of division, though not of growth; that the relation of the bacteria to their host-cells is parasitism; that it is difficult to understand how the plant as a whole can profit by an association which injures and finally destroys the cells.—J. M. C.

LUIGI BUSCALIONI,²¹ in an extensive preliminary notice, describes his studies on the development of the root in the monocotyledons. His results are new and interesting in many respects; and their early publication *in extenso* is to be desired. The author calls attention to the fact that in the root of the same species the periblem and plerome may originate from a common meristem, or have distinct and separate initials according as the root is of larger or smaller size. The medulla in the case of large roots often shows its community of origin with the cortex by the presence of raphide cells such as are characteristic only of the extrastelar fundamental tissues. The apparent medulla, which is often present in smaller roots, the author does not consider to be a true medulla, and designates it *medulliform tissue*. These results are of great interest from the standpoint of existing stelar hypotheses. The root would seem to be a specially favorable organ for the investigation of these problems, both on account of its primitive structure and the clear limitation of the primary meristems. Another novelty is the announcement that the origin of the tracheary elements of the root is centrifugal, in spite of the fact that the order of their lignification is centripetal. In the Dioscoreaceae and Asparagaceae, the mother cells of the tracheary elements are multinucleate.—E. C. JEFFREY.

L. GUIGNARD²² has added certain Solanaceae to the list of plants in which "double fertilization" has been observed. His work was chiefly with *Nicotiana Tabacum* and *Datura laevis*, although enough was seen of *N. rustica*, *D. stramonium*, and *D. Tatula* to indicate that they exhibit the same phenomenon. In *Nicotiana* the generative cell divides in the pollen grain, while in *Datura* it divides after entering the pollen tube, and in both cases the male cells are small and ovoid, or very slightly elongated. In *Datura* a remarkable change in the form of the tube nucleus was observed to occur in the tube, a very much elongated and irregular filamentous form being assumed. In both genera the tube enters a synergid and discharges, the two male cells rapidly approaching the egg nucleus and the polar nuclei. In *Nicotiana* the

²¹ Sull'anatomie de cilindo centrale nelle radice delle Monocotiledoni. Malpighia 15: 276-296. 1902.

²² La double fécondation chez les Solanées. Jour. Botanique 16: 145-167. figs. 45. 1902.

polar nuclei do not fuse until after fertilization, while in *Datura* the fusion is complete before fertilization. The usual position of the polar nuclei or the fusion nucleus during fertilization is in contact with the egg. The first division of the primary endosperm nucleus is followed by a transverse wall across the sac, dividing it into two approximately equal chambers. In *Datura* this is followed by other transverse walls, so that the sac consists of four superposed chambers. In both genera the subsequent divisions of the endosperm cells occur in various planes and are accompanied by wall formation.—J. M. C.

ITEMS OF TAXONOMIC INTEREST are as follows: GOTTFRIED LUZE (Verhandl. Zool.-Bot. Gesells. Wien 52: 304-305. 1902) has described a new genus (*Pseudocalea*) of Staphyleaceae from southeastern Europe.—LEROY ABRAMS (Torrey 2: 122. 1902) has described a new *Hemizonia* from California.—N. L. BRITTON (*idem* 123) has described a new *Hydrophyllum* from Minnesota.—HENRY EGGERT (*idem* 123) has described a new *Verbena* from Texas.—C. L. SHEAR (Bull. Torr. Bot. Club 29: 449-457. 1902) has described new species of *Secotium*, *Scleroderma*, *Cucurbitaria*, *Fusicladium*, *Illosporium*, *Phragmidium*, *Aecidium* (2), *Diatrypella*, *Pleomassaria*, *Camarosporium*, and *Haplosporella*, and has established the following new genera: *Cryptoporus* (formerly a section of *Polyporus*) and *Plectrothrix* (nearest to *Monosporium*).—E. J. DURAND (*idem* 458-465) has described new species of *Discomycetes* in *Ciboria* (2) and *Sclerotinia*.—F. LAMSON-SCRIBNER and E. D. MERRILL (*idem* 466-470) have described new species of *Argrostis*, *Elymus* (2), *Festuca*, *Sitanion*, and *Trisetum*.—ALICE EASTWOOD (*idem* 471-474. *pl.* 21) has described five new species of *Nemophila* from the Pacific coast.—SPENCER LEM. MOORE (Jour. Linn. Soc. Bot. 35: 305-367. *pl.* 8. 1902), in describing numerous new African *Compositae*, has published a new genus (*Artemisiopsis*) of *Inuloideae*.—P. HENNINGS (Hedwigia 41: 145-149. 1902), in completing his account of the Javanese fungi collected by Professor Zimmermann, has described a new genus (*Discomycopsella*) of *Leptostromataceae*.—J. M. C.

MISS BLANCHE GARDNER,²³ in studying cell division in root tips of *Vicia Faba*, concludes that the nucleolus plays an important part in heredity. The statement is made that "the nuclear thread dips into the nucleolus" at one or several points and continues so until the nucleolus transfers itself into the thread. After the nucleus has divided, nearly all the chromatin is passed back and forms the nucleolus again. The conclusion is reached that the nucleolus is not a nutritive center. "The nucleolus is, at least in large part, a mass of chromatin material packed together in rounded form during the resting stage, and during this stage it is the important chromatin center. During division it becomes transformed into chromosomes. The nuclear

²³ Observations on growth and cell division in the root of *Vicia Faba*. Contrib. Bot. Lab. Univ. Penn. 2: 150-182. *pl.* 3. 1902.

thread formed in the earliest stages of division merely serves as a path along which the nucleolus passes its chromatin." The author has evidently overlooked or failed to take into consideration the chromatin-nucleoli or karyosomes, which in well stained preparations of *Vicia* are always visible in the resting nuclei. The fact that in some forms of mitosis the true nucleolus — or plasmosome — is at the time of division entirely cast out of the nucleus into the cytoplasm, where it degenerates, has not been taken into consideration. That the nucleolus does contribute something to the chromatin is probably true, but it is very doubtful if it plays such an important part as has been assigned it by the author. The conclusion seems to be based largely on the staining reactions of iron-haematoxylin and Bordeaux red. Most cytologists now place little reliance on staining reactions.—W. J. G. LAND.

A TURNIP ROT has been under study for some time by Professor M. C. Potter of the Durham College of Science, England, and a number of articles have been published concerning it. In a communication to the Royal Society on June 12 the parasitic activity of the disease organism, *Pseudomonas destructans*, is minutely described. By direct observation it was seen to swell the wall of a healthy cell to two and a half times its natural thickness within an hour, by action of cytase which it excretes. The swelling could be recognized almost at once upon the introduction of the germs. Almost an hour, however, was required to make evident the toxic action by which the protoplasm is killed, followed by contraction and separation from the wall. The penetration of the cell wall by the bacteria was also directly observed, the time required being about three hours. All stages of this operation were well demonstrated by fixing, paraffin imbedding, and sectioning. Differential staining, using ruthenium-red for the walls and Löwit's method for the bacteria and their flagella, brought out the fact with great clearness. The enzyme secreted by the organism is incapable of acting upon the mature and old epidermis. Entrance into the plant under field conditions appears to be largely through wounds. Such an unequivocal demonstration of a bacterial disease of plants is a notable addition to our knowledge of plant pathology, and is especially interesting as it comes from across the Atlantic, where it has been, and is still, much the fashion among writers of all classes to deny that bacteria are capable of originating disease in plants.—J. C. ARTHUR.

IN A PAPER READ before the Society for Plant Morphology and Physiology, J. M. Macfarlane²⁴ gives an historical résumé of the progress of plant cytology. He classifies the problems of plant cytology as morphological, physiological, experimental, ecological, evolutionary, and taxonomic. He suggests that the nucleoplasm and general cytoplasm may be regarded

²⁴Current problems in plant cytology. Contrib. Bot. Lab. Univ. Penn. 2: 183-204. *pl.* 18. 1902.

as the vegetative substance of the cell, the chromatin granules as the highly specialized hereditary substance, and the linin as an intermediate substance which transmits hereditary peculiarities in a slow degree from the cytoplasm to the chromatin, and that the linin is in part the bearer of hereditary qualities. He considers that undue prominence has been given to the chromatin granules as the bearers of heredity. He thinks more light would be thrown on the tropisms if the cytological changes that originate or accompany them were accurately determined. He believes that the only correct guide to the evolutionary affinities of the plant groups and the development of species within these groups is to be found in the study of the morphological details of varieties and species based on the cell as the ultimate factor; also that it will not be possible to classify on a natural plan until exact information has been obtained and recorded in terms of cell life, of structural features, such as for example pigmentation of certain areas, the upbuilding of unicellular or multicellular hairs of definite structure, or the development of thickening zones, etc. When such data have been accumulated "it will be possible to classify plants on a natural plan, instead of, as now, by selecting one or two points of resemblance—not necessarily of morphological contact—as a taxonomic basis."—W. J. G. LAND.

IN A PRELIMINARY paper concerning a series of experiments now in progress at Harvard Botanic Garden, A. B. Plowman²⁵ gives some interesting results. Both soil and water cultures of seedlings subjected to as near normal conditions of temperature, light, and moisture as possible, were treated with both static and kinetic charges, through a range of potential from 0.5 to 500 volts. Seeds near the anode were killed by a current of 0.003 amperes or more, while those near the cathode were little affected or even stimulated. In both water and soil cultures of seedlings the same facts were established. In case the current was allowed to act for a sufficient length of time the ill effects were produced at all points between the electrodes, but slower in the soil cultures. With a current of 0.08 amperes or less the seedlings near the cathode showed an increase in the rate of growth. A provisional theory based on the disputed ionic theory is offered in explanation. From certain facts established by experiment the conclusion is made that negative charges stimulate and positive charges paralyze the protoplasm of young seedlings. For example, a positive charge of 500 volts killed lupine seedlings, while a negative charge of similar potential actually stimulated the plants; in water cultures subjected to a weak current of electricity the root-tips turn towards the anode. The explanation for the latter is that the side of the root toward the anode is retarded in its growth by the positive ions, while the opposite side is stimulated by the bombardment of the negative

²⁵ Certain relations of plant growth to the ionization of the soil. *Am. Jour. Sci.* 14: 129-132. 1902.

ions. Since the plant body is electro-positive to the soil, the negative electrons are being discharged to the plant in its normal physiological activity and are beneficial, while the reverse condition is detrimental.—F. D. HEALD.

THE EXPERIMENTAL MORPHOLOGY of the potato tuber has been taken up again by Vöchting.²⁶ The French variety "Marjolin" was grown in pots in garden soil. In darkness at a temperature of 6–7° C. few roots, but numerous new shoots, are developed. The latter take the form of small tubers, and never bear the small leaves normally produced in darkness. At a temperature of 25–27° C (about the optimum for growth) both roots and shoots are produced in large numbers, and the latter all have the form of normal etiolated shoots. As the temperature is decreased below the optimum, more tubers and fewer leaf-bearing shoots are produced, and in the neighborhood of the minimum for growth all the shoots are tuberous. The temperature seems to be directly effective in this response. If new tubers have begun to form in the cold, and then the culture be transferred to the optimum temperature, tuber formation ceases and the development of leafy shoots begins, to continue while the temperature is suitable. A corresponding change from the formation of leafy shoots to that of tuberous ones follows a change of temperature in the opposite direction, but leafy shoots started in the cold continue to grow as such at low temperatures. However, they change their response to the gravity stimulus entirely; while at the higher temperature they are negatively geotropic, at the lower they become positively so. The influence of the amount of water in the soil is almost as important as that of temperature. At a temperature suitable for the production of leafy shoots a culture with little water produces only tubers. When water is added to the soil leafy shoots are developed. In cultures with dry air above the soil, the leaf-bearing shoots creep along the surface of the substratum. The author concludes they are positively hydrotropic. The partial pressure of oxygen is not effective in determining the formation of new tubers or leafy shoots. But with the partial pressure of this gas the roots fail to be provided with the usual hairs.—B. E. LIVINGSTON.

COPELAND²⁷ has studied the mechanism of the opening and closing movements of stomata in a large number of forms well distributed throughout the plant kingdom. Several methods were resorted to in determining the way in which the various stomata open and close, the main one being the observation of tangential sections of the leaf. Observations of cross and longitudinal sections and of the stomata *in situ* were also made use of. Unless the methods are at fault (and there seems no reason to believe that

²⁶ VÖCHTING, HERMANN: Ueber die Keimung der Kartoffelknollen. Bot. Zeit. 60: 87–114. *pls.* 3–4. 1902.

²⁷ Copeland, E. B., The mechanism of stomata. Annals of Botany 16: 327–364. *pl.* 13. 1902.

they are), it appears that active movements of stomata are much more common than we have been led to believe. And the method of opening and closing, apparently always dependent upon an osmotic change in volume of the guard cells, is as various as are the plants in which it occurs. Absorption of water with its accompanying increase in the volume of the guard cells results in so altering the shape of these cells, by bending or stretching their walls, as to open the pore between them. The mechanical types of stomata studied are illustrated by figures and are tabulated by the author in the following scheme, which is copied from his concluding paragraph. "The pore opens by

1. A change in shape, rather than by stretching the walls, in which the change is

- (a) An increase in the depth of the guard cell, in which there is chiefly concerned the entire wall except the dorsal (*Medeola*, *Equisetum*), the inner half (*Mnium*), the outer half (*Funaria*), the dorsal half (*Lycopodium*), the ends (*Osmunda*).

- (b) An increase in the width of the slender stoma (*Sagittaria*).

2. Stretching the thin dorsal wall (*Amaryllis*).

3. A change in shape, with or without much stretching, at the ends of the guard-cells, which forces the dorsal wall, with the passive middle part of the cell, either directly backward (*Gramineae*), or upward and backward (*Coniferae*).

4. Combinations of the types of *Amaryllis* and *Mnium* (*Helleborus*), and of *Amaryllis* and the *Gramineae* (*Achillea*)."— B. E. LIVINGSTON.

SPINDLE FORMATION in *Agave americana* has been described recently by Osterhout.²⁸ Considerable attention was given to technique, especially to fixing. About forty fixing agents were tested by watching their effect upon the living cell, and it was found that some of the most highly recommended solutions produced profound disturbances in the cytoplasm. For most objects fixing agents were found which produced no visible change in the living cell, as far as could be observed with a 2^{mm} oil immersion lens during the application of the reagent; but even in some such cases the material undergoes structural changes after a few hours, and the time must be shortened accordingly. Flemming's strong mixture proved to be the best in most cases; very fair results were obtained with iridium chloride, platinum chloride, palladium chloride, and Flemming's strong mixture with an excess of chromic. Material was washed from two to eight hours in running water and then dehydrated. Mixtures of absolute alcohol and bergamot oil were used for clearing. Gentian violet was used for staining kinoplasm. If the stain washes out too readily, some gentian violet should be dissolved in the absolute alcohol. From two to twenty seconds' immersion in dilute iodide iodine solution just before transferring to the absolute alcohol often gives a sharper differentiation.

²⁸ OSTERHOUT, W. J. V., Cell Studies. I. Spindle formation in *Agave*. Proc. Cal. Acad. Sci. III. 2: 255-284. pls. 25-28. 1902.

The summary of Professor Osterhout's work on spindle formation in *Agave americana* is partly as follows: During early stages in the first division of the pollen mother cell the spindle is enclosed in a special membrane of cytoplasmic origin, which forms a complete investment around it. The functions of the membrane appear to be comparable to those of the nuclear wall and the limiting membrane of the cytoplasm. There is no web of fibers such as is usually described for this stage. The spindle-forming fibers are radial from the beginning, and are attached both to the nuclear and spindle walls. The second division differs radically from the first, the spindle formation resembling, in general, that described for the spore mother cells of *Equisetum*.

The plates are in three colors, reproducing the effect of the safranin-gentian violet-orange stain.—CHARLES J. CHAMBERLAIN.

A PHYSIOLOGICAL STUDY OF THE ANTIPODALS has been undertaken by T. Ikeda.²⁹ Investigations on *Tricyrtis hirta* form the subject of the first paper and it is expected that others will follow. Besides observations on microtome sections prepared in the usual way, microchemical reactions were tested on free-hand sections from fresh materials. The archesporial cell becomes the megaspore mother cell directly without a previous division into a primary wall cell and primary sporogenous cell; the mother cell gives rise to four megaspores, of which the one nearest the chalaza is functional. In the first division of the mother cell the chromatin forms tetrads strongly resembling those of such forms as *Gryllotalpa*, as described by zoologists. Double fertilization was observed. The endosperm does not form a parietal layer, but the nuclei are evenly distributed throughout the sac. A considerable amount of endosperm is formed before the division of the fertilized egg, one of the figures showing twenty nuclei in a single section. The chief interest in the paper lies in the microchemical investigation. In early stages no starch is found in the ovule, but as development proceeds starch appears in the funiculus and outer integument, and the outer and inner surfaces of the inner integument become cutinized except in the micropylar region. Starch then appears in the inner integument, though not as abundantly, and dextrin can be detected in the antipodal end of the sac. Just before the fusion of the polar nuclei, dextrin is evident in the micropylar portion of the inner integument and also in the antipodals and egg apparatus, while the starch has disappeared from the inner integument and appeared in the nucellus. After fertilization, the dextrin disappears from the integument and is present only in the fertilized egg, and starch has almost entirely disappeared from the integuments and is scanty in the funiculus, but after a few divisions of the embryo starch becomes abundant in the integuments and in the endo-

²⁹ Studies in the physiological functions of antipodals and related phenomena of fertilization in Liliaceae. Bull. Coll. Agric. Tokyo Imp. Univ. 5: 41-72. pls. 3-4. 1902.

sperm. The chalaza and conducting region have a soluble carbohydrate instead of starch. Microchemical tests, together with the cytological features of the antipodal cells and the anatomical structure of the neighboring tissues, lead to the conclusion that in *Tricyrtis* the antipodals are the center of absorption of raw materials, of their elaboration into the proper form, and the means of transmission of food to the proper place. The dextrin in the micropylar portion of the integument is believed to serve for the nutrition of the pollen tube, while that in the egg supplies the embryo during its early stages. The cutinization of the inner integument makes it necessary for most food material from the exterior to pass through the antipodals.—CHARLES J. CHAMBERLAIN.

OPEN LETTERS.

WEBB'S "STUDY OF SPIRAEA."

IN the June number of the BOTANICAL GAZETTE there appeared a paper by Mr. J. E. Webb under the title "A morphological study of the flower and embryo of Spiraea." In looking through it I noticed that the illustrations of the sections of the flowers represented obdiplostemonous flowers with but two carpels and a simple raceme, all characters which do not agree with the true Spiraeas. It became apparent, therefore, that the paper did not deal with *Spiraea japonica* Linn. f., but with *Astilbe japonica* Gray (*Hoteia japonica* Morr. and Decne. *Spiraea japonica* Hort.), an herbaceous plant belonging to the Saxifragaceae. Unfortunately it does not happen infrequently that morphological and physiological researches are based on wrongly named plants. Of numerous similar instances I shall mention here only one I came across a few days ago in the *Botanische Zeitung* (47: 629. 1889), where a paper by J. H. Wakker on "Bau und Dickenwachsthum von *Abrus precatorius*" is published. The figure on the plate of a flattened stem and the mention in the text of "der Gattung Phaseolus ähnliche Blätter" left little doubt that the plant under consideration was not *Abrus precatorius* but *Rhynchosia phaseoloides*, which is sometimes confounded with the former on account of the similarity of the seeds. The article was reviewed in Just's *Botanischer Jahresbericht* without the error being noticed. As also in the present case Webb's paper has been mentioned in other journals without attention being drawn to the misleading names, I thought it advisable to point out that the paper chiefly deals with *Astilbe*, and thus refers mainly to Saxifragaceae, and the *Spiraea japonica* there cited should be changed to *Astilbe japonica* Gray, and the *Spiraea astilboides* to *Aruncus astilboides*, while *Spiraea salicifolia*, with only one illustration, will remain as the correct name.—ALFRED REHDER, *Arnold Arboretum*.

NEWS.

THE BRYOLOGIST Hugo von Klinggraeff died April 1 at Paleschken, West Prussia.

DR. B. SCHMID, privatdocent at the University of Tübingen, died April 28.

PROFESSOR ANTONIO MORI, Director of the Botanic Gardens at Modena, died April 6.

MR. E. W. D. HOLWAY spent the month of September in the mountains of western Canada collecting fungi.

PROFESSOR DR. G. LEIMBACH, of Arnstadt, Thuringia, and publisher of the *Deutsch. Bot. Monatsschrift*, was missing from his home on June 11, and on June 13 his body was found at the foot of a cliff, from which he had evidently fallen.

THE LAST REPORT (13th) of the Missouri Botanical Garden shows that the mounted herbarium consists of 364,953 specimens, 23,942 of which are thallophytes. The library contains 36,016 books and pamphlets, and at present 1,133 serial publications are received.

MRS. WILLIAM STUART, of Purdue University, for some years assistant in botany to Dr. Arthur, and for the last year associate horticulturist in the Experiment Station of that institution, has been appointed horticulturist in the University of Vermont to succeed Professor Waugh, who goes to the Massachusetts Agricultural College.

THE UREDINEAE are to receive monographic treatment by P. and H. Sydow of Berlin. Gebrüder Borntraeger announce the early appearance of the first part of the work. It is to appear in parts over a period of three or four years, and will eventually form three volumes, each containing about 1,000 pages, with a large part of the species illustrated, and all known species included with their synonymy. The price will be about 60 marks per volume to subscribers.

M. J. C. WILLIS, Director of the Royal Botanic Gardens, Peradeniya, Ceylon, proposes to be absent from Peradeniya until March 1903, on a tour through England, the United States, Japan, etc., for the study of agricultural and botanical organizations in those countries. Letters on departmental business should be sent to the Acting Director, Mr. J. B. Carruthers at Peradeniya; private letters to the Royal Societies' Club, 63 St. James St., London, 1902]

S. W., till October 1st, and to Olga, San Juan co., Washington, U. S. A. till December 15th.

THE DIVISION OF FORESTRY EXTENSION, organized in the Bureau of Forestry on July 1, to supersede the Section of Tree Planting, is to have charge of all work that deals with the creation of forests where at present there are none. Field parties are now at work in New Hampshire, Massachusetts, New Jersey, Nebraska, Oklahoma, Arizona, Washington, and Oregon. In connection with the system of cooperation with private land owners in planting the Bureau of Forestry at the beginning of the present field season had arranged 224 planting plans in 172 localities of twenty-nine different states. The majority of these plans are for woodlots of individual land owners, but in some cases plans are being made for corporations, cities, and even states. The bureau has also established nurseries in the two forest reserves recently established in the sand-hill region of Nebraska. The principal species used at first will be jack pine, western yellow pine, white fir, and Colorado blue spruce. The bureau has also recently taken up a study of the tendencies of natural forests to extend over land devoid of forest growth. Field parties are now investigating the reproduction of white pine on pastures and abandoned lands in Massachusetts and New Hampshire; another field party is studying the same problem in Oklahoma in connection with the hard wood growth which composes the timber belts of that region; and a similar study is being made of the Prescott reserve in Arizona. The reclamation of shifting sand dunes has also been taken up as a problem by the bureau. The regions most severely affected are the dune regions of the Atlantic and Pacific coasts, the lake district region of Michigan, and the Columbia river district of Washington and Oregon. Two field parties are at work on this problem, the one investigating the dune district along the Atlantic coast and the other the Columbia river district.

BOTANICAL GAZETTE

OCTOBER, 1902

A MORPHOLOGICAL STUDY OF THUJA.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.
XXXIX.

W. J. G. LAND.

(WITH PLATES VI-VIII)

MATERIAL for the study of *Thuja occidentalis* L. was collected in the vicinity of Chicago during the late spring and early summer of 1901. A few collections were made in June 1902, in order to determine whether the time of fertilization varies in two successive seasons. The trees were visited twice each week and material fixed immediately after the removal of the branches. Branches were also kept in the laboratory, some having water pressure applied to the cut end of the stem, and collections were made daily. All the material from which illustrations are made was taken from a single tree, the most vigorous one to be found. Collections were made from many other trees in order to determine whether the periods of the various stages of development are the same in different individuals of the same locality. Little difference could be observed.

For stages before the formation of archegonium initials 1 per cent. chromo-acetic acid was most useful, but for later stages it was not so good, as it was not possible to secure rapid penetration of the tissues even when used at a temperature of 80°. A modification of Carnoy's formula was found to give the best results for fertilization and succeeding stages, although many fixing agents were given a thorough trial. None of the fixing

agents proved entirely satisfactory. Flemming's triple stain gave good results for pollen tubes and early stages in the development of the archegonia, but by far the most satisfactory stain was Haidenhain's iron alum-haematoxylin. Delafield's haematoxylin combined with orange G was best for embryos. Sections were cut 3 to 5 μ thick.

THE POLLEN GRAIN AND POLLEN TUBE.

No attention was given to the formation of microspores from the mother cell, their study being taken up shortly after the separation of the tetrads (*fig. 1*). The appearance of the pollen grains at the time of shedding is shown in *fig. 2*. It does not appear that prothallial cells are cut off. Methods which easily demonstrate the prothallial cells of *Pinus* and similar forms have failed to show any such structures in *Thuja*. However, considering the ephemeral nature of prothallial cells in most gymnosperms, and the small size of the microspores of *Thuja* (20 μ in diameter), it is possible, though not probable, that they may have been overlooked. So far as could be determined, the next step after the separation of the tetrads is the organization of a tube nucleus and a generative cell (*fig. 2*). The microspores of *Cupressus Benthamiana* and of *Biota orientalis* seem in every respect like those of *Thuja occidentalis*.

In material collected June 2, 1901, the pollen tube had penetrated a short distance into the nucellus (*figs. 3-4*). The generative cell had already divided, and both the tube and stalk nuclei were in advance, and close against the large body cell. One of these nuclei is invariably somewhat smaller than the other. In *fig. 4* the smaller nucleus is not shown, as it lies immediately beneath the larger one. Conspicuous protoplasmic streams radiate from the tube and stalk nuclei downward to the end of the pollen tube, but little cytoplasm is found above the body cell. The nucleus of the body cell is in general spherical and is surrounded by a thick sheath of cytoplasm (*figs. 4-5*). A deeply staining spot, presumably kinoplasmic in nature, lies in the cytoplasm. Strasburger (11) shows this spot in his

figures of Juniperus, and Chamberlain shows similar structures associated with the male nuclei of *Pinus Laricio*. The finely granular areas in the body cell of Pinus, as described by Miss Ferguson (8), and the kinoplasmic regions described by Coker (5) for the egg of Podocarpus seem to consist of the same substance. The spots, though generally present in the body cell, were not found in the male cells of Thuja. These structures are suggestive of the blepharoplasts of Ginkgo and certain cycads, and may be a survival of some such structures possessed by ancestors from which the Pinaceae have descended.

Before the appearance of the archegonium initials (June 16, 1901), the penetration of the pollen tube is relatively slow, but at this time its downward movement is much accelerated. The tube quickly pierces the remaining rows of nucellar cells, spreads itself over the mouth of the archegonium complex, and absorbs almost entirely the remnants of the neck cells, thus laying bare the upper ends of the eggs (*fig. 10*). The body cell elongates (*fig. 5*) and divides into two hemispherical cells of the same size, this division taking place immediately before fertilization. That both cells are functional is shown by the fact that when only one pollen tube enters the complex two embryos are formed. In many instances it was observed that the contents of the pollen tube, which was in advance of the others, had fertilized two eggs. The equal size of the male cells is another evidence that both are functional.

Arnoldi (1) finds in *Cephalotaxus* the two male cells of the same size. Strasburger and also Belajeff (3) figure the male cells of Juniperus as equal. Arnoldi's (2) figures of the male cells of Sequoia show them to be equal. According to Coulter (6) the male cells of *Pinus Banksiana* are alike in size and volume. Chamberlain (4) finds the same to be true of *Pinus Laricio*. In cycads male cells are equal. Belajeff (3) observed that in *Taxus* one of the male cells is much smaller than the other and does not enter the egg at all. Coker (5) finds one functioning male cell in Podocarpus. In *Pinus Strobus* Miss Ferguson (8) reports them as unequal, with the larger cell invariably in advance.

There can hardly be any doubt that the occurrence of two equal male cells is more primitive, and that any difference in size or loss of function is a more specialized condition. It seems reasonable to suppose that both male cells are functional in all forms which have archegonia collected in a complex, for there is nothing to prevent each male cell from reaching an egg. In forms where the male cells are unequal in size the archegonia are scattered, thus making it practically impossible for the second male cell to function, and this will of course account for the reduced size.

Three to four pollen tubes appear to be the normal number in *Thuja*. They either pursue different routes through the nucellus or pass down side by side. In the latter case, one has its tip in advance of the others. In numerous instances it was observed that when the eggs fail to function, as they frequently do, the pollen tube penetrates to the bottom of the complex and in some instances pierces the jacket cells. When this occurs the male cells increase very much in size as the tube nears the bottom of the archegonium complex (*fig. 7*). In one instance the cells were 50μ in length. The longer diameter of the hemispherical male cell at the time of fertilization is in general 20μ .

DEVELOPMENT OF THE ARCHEGONIUM.

Early stages in the development of the endosperm were not studied, but the process seems to be similar to that described by Jäger (9) for *Taxus*.

The archegonium initials are differentiated about the middle of June, their number being usually six. They rapidly elongate, become conical, and as yet have very little cytoplasm (*fig. 8*). The nuclei move toward the outer end of the initials and the neck cells are cut off (*fig. 9*). So far as could be determined they are cut off simultaneously. Each neck cell divides by anticlinal walls, forming from two to six cells, and there is no periclinal division. Almost immediately after the last anticlinal wall is formed the neck cells begin to disorganize, and they are soon almost entirely assimilated by the central cells, which at this time are increasing in volume at a very rapid rate.

About the time of the cutting off of the neck cells, the jacket cells appear. At first they are poor in contents, but soon become filled with dense cytoplasm, and the adjacent layer of prothallial cells also shows a marked increase in activity. Protoplasmic connections between the jacket cells and the central cells were not seen, but it is possible that they were overlooked owing to the extreme thinness of the dividing wall. It is not believed that the nuclei of the jacket cells pass into the central cells, as reported in *Cephalotaxus* by Arnoldi (1).

Shortly after fertilization the jacket cells break down, and in many cells the chromosomes become separated, and are then in a favorable condition for counting, the gametophyte number being twelve.

After the neck cell has been cut off, the nucleus of the central cell lies very close to the upper end of the cell (*fig. 10*) and enlarges so much that its longer diameter is sometimes more than four-fifths of the diameter of the egg. A large vacuole (*figs. 10-11*) now rounds out in the center of the cell. Cytoplasmic masses collect at each end of the central cell, and are connected with each other by a thin layer at the periphery of the central cell. Two deeply staining masses, presumably kinoplasmic in nature, are present. The one near the nucleus resembles somewhat the mass mentioned in connection with the body cell, but it is not so sharply limited. The other, in the lower end of the egg, sometimes stains so densely that it often resembles an overstained nucleus.

At this stage the tip of the pollen tube is in the mouth of the archegonium complex, and is separated from the central cells by remnants of the neck cells.

THE VENTRAL NUCLEUS.

Karyokinetic figures showing the cutting off of the ventral nucleus were obtained in material fixed June 20, 1901, and June 16, 1902 (*fig. 12*). It takes a position at one side of and a little above the egg nucleus, almost in contact with the wall of the egg, and usually on the side nearest the center of the arche-

gonium complex. It is not separated from the egg by a wall, but lies free in the cytoplasm of the egg. The figures of Strasburger (11) and Belajeff (3) show that it takes a similar position in *Juniperus*.

Arnoldi (2) claims that there is no ventral canal cell in the Cupresseae, and among the Taxodieae he failed to find it in *Cunninghamia*, *Sequoia*, *Cryptomeria*, and *Taxodium*. Coker (5), however, finds a ventral nucleus in *Taxodium*, although it is not separated from the egg by a wall, lying free in the cytoplasm of the egg. He also finds the ventral nucleus very prominent in *Podocarpus*, but here also no wall is formed. Strasburger (11) as long ago as 1879 figured the spindle in *Juniperus*. There can be no doubt that the free ventral nucleus without a separating wall is a specialized condition. A similar reduction in the neck canal cells can be seen as one traces a series through the bryophytes and pteridophytes. In most of bryophytes the number of neck canal cells is rather large; in the pteridophytes the number has become small, often only two, and even here a wall seldom forms between the two nuclei. In most gymnosperms there is a definite ventral canal cell, cut off by a conspicuous wall; in *Taxodium*, *Podocarpus*, and *Thuja* the nucleus is formed, but the wall is suppressed. This may be the case in the forms described by Arnoldi (1, 2), and may have led him to think that the ventral canal cell was not represented. We doubt whether a ventral canal cell is lacking in any gymnosperm, and believe that the absence of such a cell, or at least a nucleus representing it, could be established only by the most indubitable evidence.

When an archegonium has not been fertilized, there are indications that the ventral nucleus divides (*fig. 13*). Coker (5) holds that in *Podocarpus* these divisions are amitotic. In *Thuja* after fertilization there are frequent instances of a further division of the ventral nucleus, and these divisions are mitotic. Coulter and Chamberlain (7) suggest that in some cases the ventral nucleus in *Pinus* may be fertilized instead of the egg. A number of the writer's preparations of *Thuja* lead him to believe that both the ventral nucleus and the egg in the same archego-

nium may be fertilized. In *fig. 17* the proembryo is well advanced, while the ventral nucleus has formed a group of four cells — three of which are shown in the figure, as it was drawn from a single section — which certainly suggests a proembryo in the four-celled stage. Another preparation shows eight cells with indications that walls are soon to appear. The probability of such a fertilization is strengthened by finding occasionally in the same ovule embryos growing upward into the nucellus (*fig. 27*), as well as downward into the endosperm. These embryos are so old that it was not possible to determine definitely if their suspensors are connected with a common archegonium, but such appears to be the case. The embryos growing upward into the nucellus are not so vigorous as those growing downward into the endosperm.

FERTILIZATION.

The contents of the pollen tube are discharged into the space immediately above the archegonium complex, but it does not appear that very much enters the egg. Traces of the cytoplasmic contents of the pollen tube can usually be seen in the upper end of the egg, usually showing as densely staining masses. In some cases the tube and stalk nuclei enter the egg, in others only one of these nuclei enters, but in the great majority of cases they do not enter the cytoplasm of the egg at all, but disorganize in the space above the archegonia. *Fig. 14* shows the male cell entering the egg. At this stage, in general, the large vacuole which occupied the center of the egg has disappeared, and the egg nucleus has taken its place. Soon after coming in contact with the egg the male nucleus slips from its sheath and moves downward toward the egg nucleus. The actual breaking out of the male nucleus from its cytoplasmic sheath was not observed, but numerous preparations showed remnants of the sheath in the upper end of the egg. *Fig. 15* shows the male cell just after its escape from the sheath, and also shows one of the rare cases in which the large vacuole is still present at this stage. The male nucleus passes down, and

on coming in contact with the egg nucleus presses the side of the latter inward (*fig. 16*), and finally fuses with it. A close series of stages covering the period from the escape of the male nucleus from its sheath to final fusion was not secured. The time from the rupture of the pollen tube to the formation of the fusion nucleus is very short. Ovules taken on June 20, 1901, from a twig bearing perhaps a dozen cones, showed all stages from the formation of ventral nuclei to well developed suspensors. Not infrequently a male cell in contact with the tip of an egg, and proembryos of four cells may be found in the same complex.

THE PROEMBRYO.

The fusion nucleus is in general below the center of the egg, and remains in this position until the first division is completed. The dividing nucleus is surrounded by a mass of deeply staining cytoplasm (*fig. 18*), which as the spindle disappears closes in between the two nuclei and envelops them, as shown in *fig. 19*. The spindle, as in the first division of the egg in other gymnosperms, is intranuclear. When the two nuclei are in the stages shown in *figs. 19-20*, the cytoplasm above begins to thin out, showing in many instances a vacuole-like space between the ventral nucleus and the proembryo. This space is never entirely free from cytoplasmic masses. In some preparations, as well as in all later stages, it appears more like a break in the continuity of the cytoplasm than like a vacuole (*figs. 22-23*).

The two nuclei sink to the bottom of the egg, lose their rounded form (*fig. 20*), and divide simultaneously (*fig. 21*); while the ventral nucleus has enlarged considerably (*figs. 22-23*) and is quite conspicuous.

The four nuclei resulting from the second division of the proembryo usually arrange themselves in pairs, as shown in *fig. 22*, which is reconstructed from serial sections. The third division of the proembryo is also simultaneous (*fig. 23*), and gives rise to eight free nuclei, and walls appear shortly after this last division. Among the cycads and in Ginkgo, after fertilization, there is a long period of free nuclear division before any

walls are formed. In *Podocarpus* sixteen or thirty-two free nuclei are formed; and in *Taxus* and *Cephalotaxus* a like number. In *Thuja* the number of free nuclei is constantly eight, while in *Pinus* and its allies the number is only four. Even so small a number as two is reported by Strasburger (11) as occasionally occurring in *Ephedra*; and in *Gnetum*, according to Lotsy (10), there is no free nuclear division at all. It would seem that there is a gradual transition from an extensive free nuclear division to a condition in which the first division of the egg is followed immediately by the formation of a wall. In the development of the embryo *Thuja* has not advanced so far as forms like *Pinus*, although in its cyclic arrangement and in the reduction of the male gametophyte it has proceeded much further.

A wall transverse to the long axis of the oospore now separates the eight nuclei into two groups, each group having four nuclei. The nuclei of the lower group are completely walled in, and from these the embryo develops. Walls parallel to the long axis of the oospore extend from the transverse wall upward a short distance into the cytoplasm of the oospore, thus walling in the nuclei on three sides, but leaving them freely exposed to the cytoplasm above (*fig. 24*). The ventral nucleus is still visible but shows marked signs of disintegration.

The four nuclei of the upper group now divide simultaneously, and walls are formed transverse to the long axis of the archegonium (*figs. 24-25*). The proembryo at this time consists of twelve cells; two tiers of four cells each, and the group of four in the tip, which were formed at the time shown in *fig. 23*. The upper tier of incompletely walled nuclei, produced by the division shown in *fig. 24*, soon disintegrate. The second tier rapidly elongates and forms the four suspensors (*fig. 26*).

A single embryo is developed from the lowest group of cells, which is thrust downward by the suspensors. In the *Abietaceae* each cell forms an embryo. Coulter (6) has shown that in *Pinus Laricio* two embryos may develop at the end of a single suspensor. In *Thuja* there is a tendency to form two groups of cells. The line of division is clearly apparent in the earlier

stages of the embryo, especially in cross sections (*fig. 28*). The line of division disappears as the embryo becomes older.

My acknowledgments are due to Professor John M. Coulter, and Dr. Charles J. Chamberlain for assistance rendered during the progress of the work.

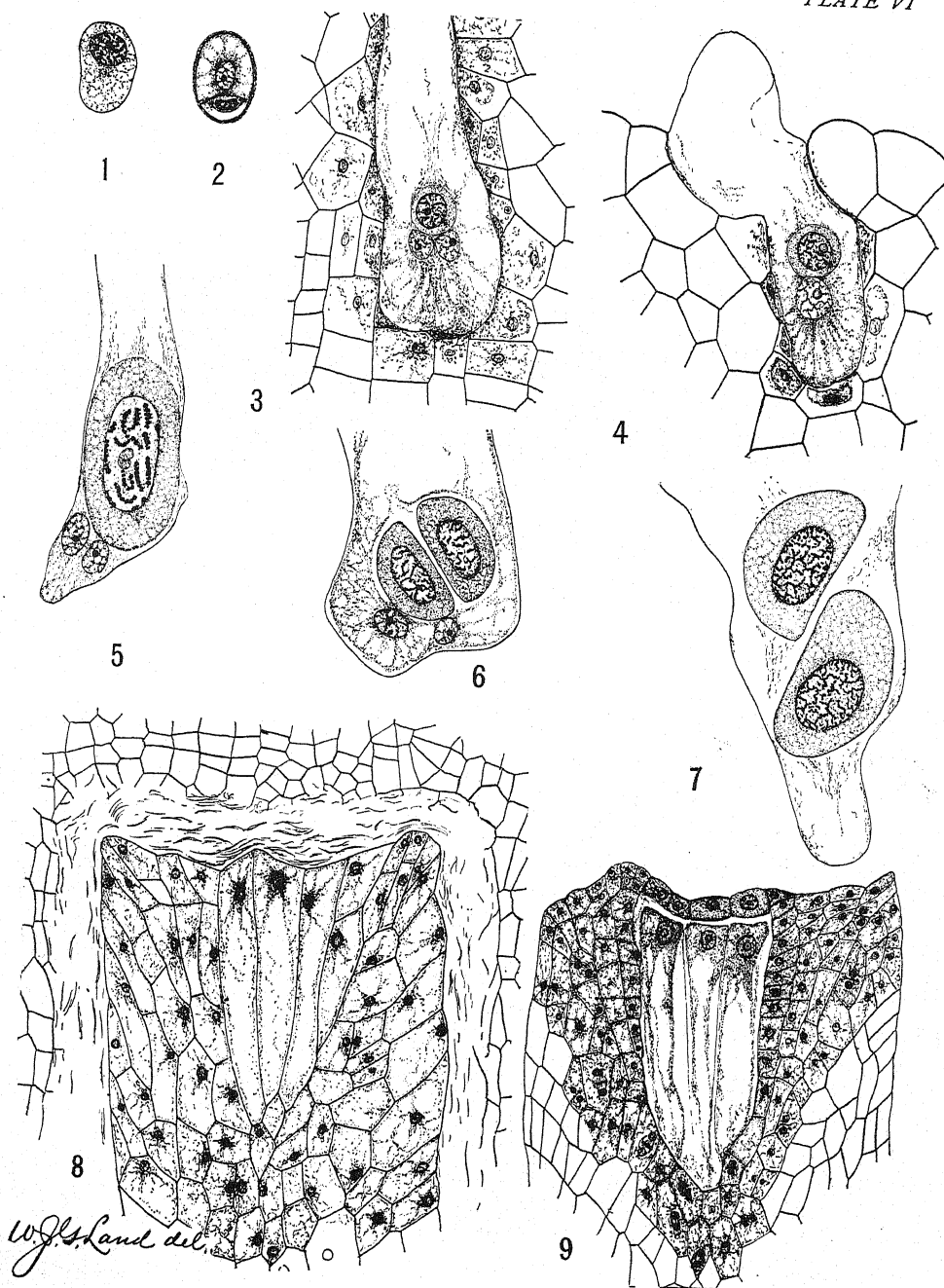
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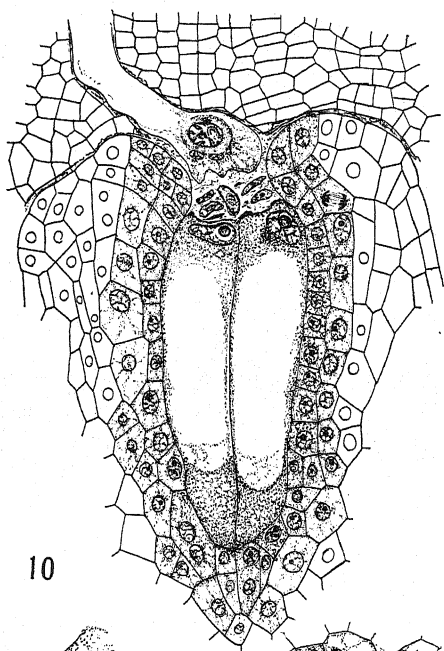
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EXPLANATION OF PLATES VI-VIII.

The figures, with the exception of *figs. 8, 9, 10, 11, and 28*, were drawn with Abbé camera lucida, Bausch and Lomb $\frac{1}{2}$ objective and ocular 2. For *figs. 8, 9, 10, 11, and 28* a Bausch and Lomb $\frac{1}{8}$ objective and ocular 2 were used. The magnification of *figs. 8, 9, 10, 11, and 28* was 450; all others 850. The plates are reduced to one-half the original size. The abbreviations used are: *b*, body cell; *v*, ventral nucleus; *m*, male cell; *o*, egg nucleus; *s*, suspensor



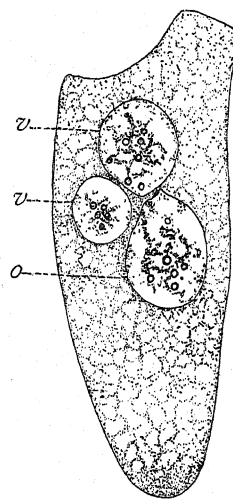
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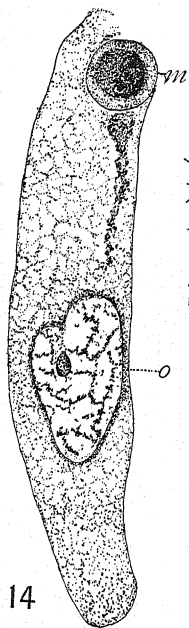
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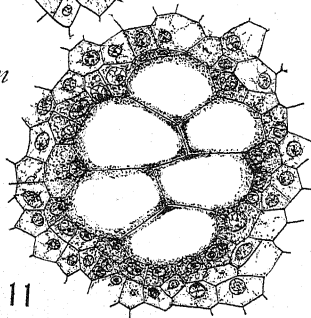
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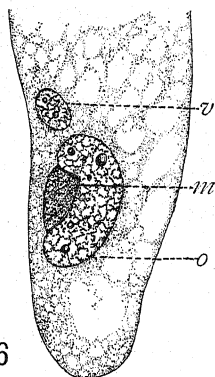
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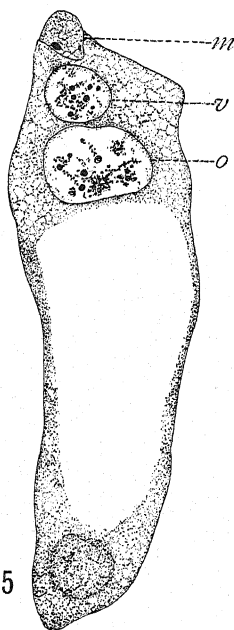
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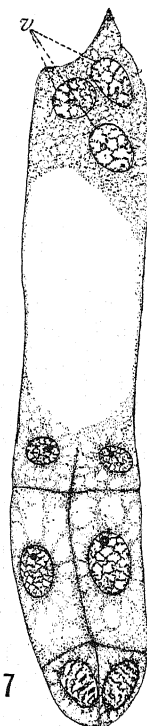
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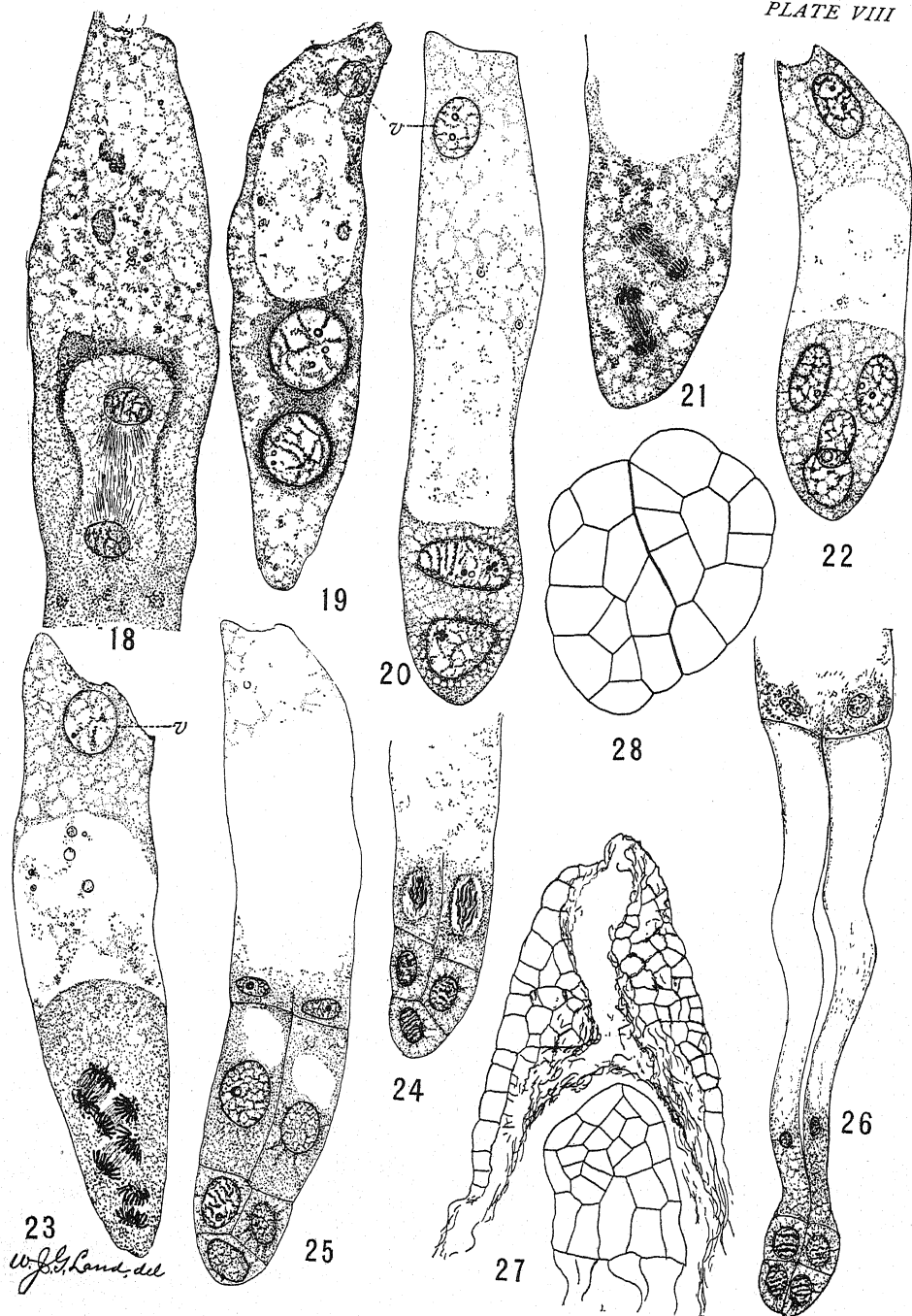
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W. J. Land, del. 16

LAND on THUJA



LAND on THUJA

- FIG. 1. Pollen grain shortly after separation of tetrad.
FIG. 2. Pollen grain showing tube nucleus and generative cell.
FIG. 3. Pollen tube with tube and stalk nuclei in advance of the body cell.
FIG. 4. Pollen tube entering nucellus.
FIG. 5. Body cell preparing to divide.
FIG. 6. Tip of pollen tube with two male cells and tube and stalk nuclei.
FIG. 7. Male cells at the bottom of an archegonium which failed to function.
FIG. 8. Longitudinal section through upper end of prothallium, showing archegonium initials.
FIG. 9. Archegonium complex after neck cells have been cut off.
FIG. 10. Archegonium complex just before cutting off the ventral nucleus; jacket cells very active, neck cells disintegrating, and body cell preparing to divide.
FIG. 11. Transverse section through middle of an archegonium complex, showing the large vacuoles.
FIG. 12. Cutting off the ventral nucleus.
FIG. 13. Probable division of the ventral nucleus.
FIG. 14. Male cell entering the egg.
FIG. 15. Male nucleus after slipping out of its cytoplasmic sheath.
FIG. 16. Male and female nuclei in contact.
FIG. 17. Division of ventral nucleus in upper end of oospore; only three of the four nuclei shown; below is the proembryo, with the suspensors beginning to elongate.
FIG. 18. Division of the fusion nucleus.
FIG. 19. The two nuclei resulting from the division of the fusion nucleus; the ventral nucleus is above.
FIG. 20. The two nuclei at the bottom of the egg.
FIG. 21. Second division of the proembryo.
FIG. 22. Four nuclei resulting from the second division; the ventral nucleus above.
FIG. 23. Third division of the proembryo; this figure shows the last simultaneous division of the nuclei.
FIG. 24. Upper tier of nuclei dividing to form suspensors.
FIG. 25. Second tier elongating into suspensors.
FIG. 26. Suspensors, with embryo.
FIG. 27. The most advanced one of a number of embryos growing upward through the nucellus; in the preparation from which the figure is drawn there are the usual number of embryos growing downward.
FIG. 28. Transverse section of an embryo, showing bipartite appearance.

THE RISE OF THE TRANSPIRATION STREAM: AN
HISTORICAL AND CRITICAL DISCUSSION.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.
XXXVIII.

EDWIN BINGHAM COPELAND.

[*Concluded from page 193.*]

VIII. The theories ascribing the rise of sap to the atmospheric pressure and to differences in the tension of gas within the wood are not fundamentally distinct. It is true that Böhm felt called upon to drop the former when he accepted the latter; and R. Hartig advocated the latter while altogether discrediting the other. But if the living cortex of the root be regarded as inactive, it is clear that an excess of pressure outside will force water into the root, just as surely as it will make it move in the wood toward the point where the pressure is least. This is realized in dead roots, which, as is well known (Saussure; Hansen; Janse; Böhm, 1889), can temporarily at least supply the demands of transpiration. In the living root the influence of the atmospheric pressure must be the same; it may be opposed by friction or aided by osmosis; but in itself, so long as there is water outside the root and the pressure within is less than an atmosphere, it will push the water inward. Pressing water into the root must directly or indirectly press other water up the stem. The cortex of the root is easily permeable to water; and water outside but in contact with it will be subject to and will transmit the full pressure of the atmosphere. There is, therefore, no foundation for the idea (Strasburger, 1893: 55; Goppelsroeder, 1901: 211) that the atmospheric pressure cannot operate to raise the transpiration stream merely because the walls obstruct the passage of the air itself. When root pressure is not active the atmospheric pressure is probably the chief cause of the passage of water into the root; at least this conclusion is indicated by the excellent work of

Vesque (1884), who found the absorption by oleander roots to be proportional to the pressure, both below and above one atmosphere. *Vicia* was found less sensitive to slight differences in the pressure, whence it appears that osmosis plays a larger part in its absorption of water.

The atmospheric pressure theory says that the water-conducting structure of a tree is something like a large water barometer. When water is withdrawn from the top of it to be evaporated, the atmospheric pressure against the bottom forces water up to make good the loss. The water column, instead of being continuous, is broken by bubbles, each supposed to have a tension corresponding to its height in the column. The tension of these bubbles will cause a local movement, and their elasticity will make any adjustment of a disturbance gradual, so that the dependence on the atmospheric pressure is not immediate, but ultimate (and entire).

The evidence for this theory, aside from Vesque's work, which has never been adequately appreciated, is chiefly the presence of rarefied air in the tracheae. We have already dwelt sufficiently on the extent of this rarefaction. The theory demands that there be an uninterrupted decrease in the tension of the air from below upward; this must hold, however, only in each individual water-path, and need not be at all true of the tree as a whole. R. Hartig (*Die Gasdrucktheorie*) is quoted as reckoning the difference in tension sufficient to move water between adjacent tracheae at 0.00004 atmospheres, and as making elsewhere an even lower estimate. Manometric determinations of the tension are practically valueless unless it is certain that they are made in the same path. All that has ever been proven (R. Hartig, *Bot. Zeit.* 1883, among others) is that the tension is on the whole less near the top of the tree, near where the water evaporates, than it is lower down. There is no sound experimental evidence that in any single water-path of any tree there is a constant increase in pressure all the way down to the roots. But on the other hand, the fact (Strasburger, 1893: 61-63) that in the crown of the tree differences in tension depend upon the intensity of the transpira-

tion, but not on the height, is not an objection to the theory, because in the crown there must be a poor opportunity to test the tension in the same path twice; and the transverse equilibration of tensions is limited even in *Tilia*, where it is easiest.

The time and place of the occurrence of low tensions in trees permit no doubt as to their being the result of transpiration. They occur in the youngest wood, whence the water is drawn to the leaves; and they are greatest in the summer season of most active transpiration, in spite of (and also as a cause of) the fact that absorption by the roots is most active then. The usual daily variation is very conspicuous. In mosses with specialized conducting strands energetic transpiration results in the same way in the appearance of greatly rarefied gas (Haberlandt: 1883, and 1886: 416). Not only is it a general rule that the tension is lower during the day, but in many cases the tension exceeds an atmosphere by night, giving way to a relative suction when transpiration becomes active, as was mentioned in discussing root pressure. In our climate this occurs in summer only in herbs, but Molisch (Ann. Jard. Bot. Buit. 1898) reports it in lofty Javanese woody plants.

That the lower tension following transpiration will have as its result a forcing up of water from below until the tension is at least in part eliminated is almost self-evident. I do not recall seeing this questioned, except in one or two passages by Strasburger. After finding that branches of *Taxus* and *Tsuga* can absorb water under almost no outside pressure, he denies (1891: 796) that the tension of bubbles in the wood has any importance. And in speaking of the possibility of low tension in the upper part of a tree (1893: 60), where he says "So müsste für diese Erscheinung eine andere Ursache als die der Wasserhebung gesucht werden," I am uncertain what "Ursache" may mean. But in many places Strasburger takes the other view. For instance (1891: 871), "Die auf tracheler Saugung beruhende Wasseraufnahme aus dem Boden kann dann (after transpiration ceases to be active) fort dauern, bis dass die Bahn mit Wasser gesättigt ist," and (1893: 81) "Vor allem muss aber die negative

Gasspannung, die in solchen (zeitweise entleerten) Bahnen herrscht, zu deren Wiederfüllung beitragen. Ihr Einfluss dürfte stets dominierend sein."

That transpiration and absorption are not parallel has always been inexplicable except on the basis of a storing up of the "suction" (rather, reduced tension) by the rarefied gas in the tracheae. And this involves the assumption that the differences in tension suffice, in practice if not in theory, to lift the water.

The one great objection to this theory is that the pressure of one atmosphere at sea level is equal to that of a column of water only 10^m high, which is no considerable part of the height of large trees. The bare dogma "it cannot be" is not instructive nor stimulating, but has been much too effective in discrediting this theory. The atmospheric pressure certainly cannot cause an upward flow of a continuous column of water more than 10^m high; but except when root pressure is active and can act with the atmospheric pressure, it may well be doubted if such a column of water ever occurs in trees. The atmospheric pressure would be ineffective against it solely because its downward pressure would be greater. But it is well known that pressures in excess of an atmosphere never are found in actively transpiring trees.¹ At whatever height the pressure in the tree may be tested, it is always found such that the local application of a counter pressure of an atmosphere would move the water present upward. The problem is to explain how a pressure of one atmosphere decreases so gradually that it does not become zero in several times 10^m height of water, air, and wood. Denying the possibility has distracted attention from the real question. The conclusion of this paper will be occupied with this problem.

IX. The belief that the forces operating below—atmospheric and root pressure—and the tension of whatever kind arising from evaporation by the leaves were altogether inade-

¹For the explanation of Figdor's (1898) apparent discovery that high pressures are the rule in the tropics, see Molisch (1902: 53-55; also Gregor Kraus, 1895: 216). A. N. Prentiss is referred to by Clark (1874: 190) as telling of trees in Brazil which, if cut during the dry season, suck in air "so forcibly as to cause a sound, amounting almost to a groan."

quate to explain the ascent of sap left the one obvious alternative of some motive agent distributed along the stem. The only modern theories along this line making any pretence at completeness have sought this intermediate force in the activity of living cells. There are two distinct theories of this kind, proposed respectively by Westermeier and Godlewski. According to Westermeier's theory, the living cells constitute the chief path of the transpiration stream, and their osmotic activity furnishes the motive power. The vessels, and even some intercellular spaces (1884:1106-10), serve as reservoirs or landings for the water, its running down in them being prevented by capillarity. The limit on the height to which the water can well be carried at a stretch in the parenchyma alone is placed by Westermeier at 3^{cm}. It is not shown in detail that the structure of any tree is such as this theory demands; still, the association of tracheae and parenchyma is a striking phenomena, from which, in fact, Westermeier got his idea. Such rapid movement by osmosis in living cells as this theory provides for is known nowhere else.

Godlewski's theory is in better accord with the generally accepted fact that the tracheae are the chief path of the transpiration stream; he holding that the water passes through living cells, the medullary rays, only at occasional intervals, receiving each time an impulse like that of root pressure, which carries it some distance up in the tracheae. Godlewski's idea was that the water moved upward instead of falling in the tracheae, when forced into them by living cells, because of differences in the tension above and below; which would make this theory subject to the same limitations as if the living cell feature were omitted (Zimmermann, 1885). Janse (1887:34-48) sought to obviate this difficulty by ascribing the water's failure to sink to friction. There is no escaping the fact that water will sink in wood (unless hindered by too much air) by its own weight. For this explanation to hold it would be necessary then for the living cells to raise the water faster than it could run back, which is not to be expected of osmosis, and would be very wasteful at best.

Janse suggests that the medullary rays will always pass water in the same direction, being able to distinguish the upper end by virtue of the stem's "polarity." But the weight of evidence ever since Hales has been that the water moves with equal readiness in either direction (Hoffmann, 1850: 842; Hartig, 1861: 22; Unger, 1868: 397; MacNab, 1874: 363; and Böhm, Ber. Deut. Bot. Gesell. 1890. On the other side Rauwenhoff, Reinhold, and Meyer, 1897, the latter only *contra* Böhm's work). In view of the fact that the transpiration stream does not become more concentrated as it rises, the mechanism of its propulsion must be different from that we have found most likely in root pressure. Godlewski, therefore, embraces Pfeffer's suggestion that a stream may be driven through a cell if a difference in internal concentration be constantly maintained; and he seeks the energy to keep up this unequal distribution of solutes within the cell sap in respiration. The expensiveness to the plant of this operation is evident.

Aside from the isolated instance reported by Janse (1887: 30-32), in which the path of eosin carried by the transpiration stream seemed to traverse the medullary rays, the positive experimental evidence used to prove the activity of living stem cells is that "root" pressure is greater farther up than at the base of a stem, and that rootless parts of plants bleed. Baranetzky (Abh. Naturf. Gesell. Halle 1873: 51-53) is authority for the greater pressure higher up, but he experimented with only four individual *Helianthus* and *Ricinus* plants, too few to guarantee the results; and Detmer (1877. cf. Wieler, 1893) reached the opposite conclusion. I have found the pressure of *Helianthus* higher on the whole when the seedlings are cut near the ground, but have tested only a dozen plants.

Baranetzky (*l. c.* 53) also cut a piece fifteen feet long out of a maple stem, closed both ends, cut a series of wounds in it, and peeled the lower end and set it in water. After eight days the wounds, especially the lower ones, began to bleed daily, from 11 A. M. to 1:30 P. M. It was exposed to the sun from 10:30 until evening, and in spite of the fact that the temperature in the

shade rose until 3 P. M., it is possible enough that its bleeding was coincident with its hours of becoming warmer. That the sap became bitter and astringent shows that its extrusion was not due to any normal activity of living cells; but the true explanation is probably the same as that of Pitra's experiments. Pitra made numerous experiments differing from Baranetzky's in that the piece of a stem was submerged except the upper end, which was provided with a manometer. Bleeding was likely to begin after eight or more days. Pitra had here substantially the same physical apparatus as an osmometer. The sap in the wood is slightly more concentrated than the water outside; between them the cambium or youngest immature wood would be a very imperfect semipermeable membrane, and the callus or healing tissue formed in and over the exposed surface within a few days (cf. Molisch, 1902; Wieler, 1893: 150) would make a much better one. A continuous layer of uninjured cells between the sap and the water would insure success; accordingly when the leafy branch was immersed and the cut end, with the manometer attached, was above the water, a pressure was more certain to be developed. This experiment shows also that in such experiments the water moves toward the base of the stem just as well as toward the leaves. Wieler (1893: 30-33) has repeated these experiments, likewise making an osmometer each time, so that his results are most naturally construed as having no bearing on the normal movement of the transpiration stream. C. Kraus has published an enormous number of instances of so-called bleeding from various isolated parts of plants. In at least a part of these the conditions were such that by the formation of a wound tissue an osmometer was formed. I have not had access to all of C. Kraus' work, but what I have seen makes me quite ready to accept the opinion of Molisch that the extrusion of water was always a direct or indirect effect of wounding, and without any relation to the rise of sap in healthy plants. Molisch's own work (1899) on the voluminous bleeding of sugar producing palms was more of a puzzle in the absence of information on the histogenetic results of the wounds inflicted, until his paper of

1902 classing this with the work of Pitra, Böhm (1892), and C. Kraus. Looked at in this way, we have here a complete layer of live cells formed across the water conducting tissues, making still another osmometer²—an enormous nectary. The water being drawn into this nectary from the conducting elements by osmosis, it is exactly the same, so far as concerns the problem of the ascent of the water, as though it were drawn by the same force into the transpiring cells of the leaf.

Strasburger, who can speak with most authority, says the structure of many trees, notably *Dracaena* (1893:17), is much less favorable to the action of living cells than is that of gymnosperms, which were Godlewski's chief subject of discussion.

The most conclusive argument against the activity of living cells in the ascent of sap is its moving freely upward in stems where the cells have been killed by poisons or by boiling. More or less injurious stains have always been used to detect the path of the transpiration stream. Of more violent poisons, K_3FeCN_6 was carried up in experiments for the same purpose by Rominger, Hoffmann (1848; 1850:796,842), Von Mohl (1851:231), and Van Tieghem (118 *seq.*) Boucherie (1840), in experiments in which the poisons must have risen more than 10^m, had various ones absorbed, especially iron pyrolignite. This was also carried up more than forty feet in an experiment already described by T. Hartig (1853:313), and was afterward carried downward in a reversed transpiration current in an experiment by the same author (1861:23). Saussure (1804) let $CuSO_4$ be absorbed, which killed the plants after a few days. Dutrochet (1837:214) found that H_2SO_4 strong enough to discolor them would rise in stems; from which he did not fail to conclude that living cells were unnecessary to its movement. Strasburger's work on the conduction of poisons culminated with an experiment (1893:10-17; other work, 1891:607-625) in which picric acid rose 21.9^m in an oak.

Experiments in which boiled parts of plants conducted water

² Osmometers, so-called, are not commonly used as real "measures" of osmosis; osmoscope would be a much better word.

have been made by Hansen, Weber, Janse (1887:21), Böhm (Bot. Centralb. 1890; 1892 II; 1893), Vesque (1891:583), and Strasburger (1891:645 *seq.*). Strasburger boiled the lower 12^m of a 15^m high *Wistaria*, after which water rose at least 10.8^m from the base. When part of a stem has been boiled, the living part above it usually wilts after a few days. Weber found—and Janse confirmed it—that the living part above, or both above and below, the boiled part had become impervious by the growth of tyloses, or other healing devices, such as would be used to cut off an injury arising in any other way. It is, then, the activity of the live part, and not any inactivity of the killed part which is the immediate cause of the stoppage of the transpiration stream. There is no direct evidence that any activity of living cells is necessary, even to keep the dead conducting elements in lasting proper condition.

It was never more difficult than it is now to say safely that any performance is not possible by living cells. But it has been most thoroughly proven that their assistance is in no way necessary in the ascent of sap; it is therefore exceedingly improbable. More than this, it is evident that if water be withdrawn from any vessel by living cells and returned to the same vessel higher up, or to any other vessel in easy communication with it, the water will run down again unless it be prevented by friction or by some force outside the living cells. Friction is not available, since water will sink in wood by its own weight; and without friction, a force which can hold it from running down can also draw it up, without any help from the living cells. The work of living cells in lifting water can be effective only when these cells form a closed layer without a leak. Root pressure is made possible by the presence of such a layer of cells. But an unbroken layer of living cells across the entire path of the transpiration stream, or even across so much of it as supplies water to a single leaf, is unheard of in the stem of any plant. It is the tracheae which are uninterrupted. It is precluded by its structure, then, that the stem of any plant should serve in the elevation of sap as the root does in setting up root pressure.

When Pfeffer (1892:258-267) attacked the problem of the rise of sap, by the method of eliminating impossibilities, Strasburger had cut out the assistance of living cells as this last resort; though Pfeffer was so reluctant to be left without any that he questioned the sufficiency of Strasburger's proof. As far as Pfeffer reached any conclusion, it is this (260): "Ohne irgend eine bestimmte Voraussetzung über die Mechanik der Wasserbewegung in den Leitbahnen, kommen wir also zu dem, übrigens auch schon aus anderen Argumentationen gezogenen Schlusse, dass das Wasser anderweitig, d. h. durch in den Leitbahnen entwickelte Kräfte, in die Höhe geschafft und somit das in solcher (!!) Weise auf höheres Niveau gehobene Wasser den aus den Gefässbündeln schöpfenden Zellen geboten wird." "Wie aber im Näheren der Betrieb zu Stande kommt, ist gänzlich unaufgeklärt."

X. Of the various theories on the ascent of the sap we have found no other to have so much in its favor, logically and empirically, as that which says the ultimate cause of the upward movement of water in the wood to replace the loss by transpiration is the pressure of the atmosphere against the water absorbed by the roots. To the sufficiency of this theory it is objected that at most the atmospheric pressure can push water up only 10^m , and this objection is not refuted, but rather better applied, when it is pointed out that the downward pressure of water actually occurring in transpiring trees of whatever height is never such that one atmosphere cannot overcome it. The kernel of the whole problem is, why is this atmospheric pressure exhausted so slowly with the ascent of the tree that, whatever height is reached, and however rapidly and forcibly water may be drawn from the wood, some pressure always remains?

Vesque (1884:195) proposes that in measuring the 10^m which the atmosphere can push up only the indices of water between the bubbles should be counted, for the bubbles have no effective weight. The suggestion is good as to water at rest; and would be valid and final as to the rising stream if the bubbles moved with the water; then our problem would have been

solved by Malpighi. But the bubbles do not move. As Vesque himself was first to show, the water moves past the bubbles, without as a rule disturbing their position. In the present state of our knowledge, this seems to require that liquid water be always continuous from one index of it to the next along the wall. If the pull from the leaves is operative around the bubbles, there is no known reason why that of gravity should not be. But if it were, the total pull of the water in the stem would seem to have to be equal to that of an unbroken column of water of the same height. And no such pull can be detected.

Every feature, active or structural, of the environment of the water in the wood is a part of the complex whose composite result is the rise of the water. Modifying any of these features must influence the movement of the water. Of two physiological factors—removal of the water by transpiration, and the pressure of the atmosphere—we know that in the entire absence of either the water does not rise. Any theory which leaves out of consideration any part of the environment of the water might reduce the rise of it to an equation, but would not prove its right to acceptance. The atmospheric pressure theory, taken alone, is in this negligent position. To be complete, it must reckon with the tensions, surface or other, and with the friction, external and internal, of water moving in the lumen, against the walls, and at times in the walls of the wood. Absolute completeness, such as would explain the rise of water in beech but not in oak wood, is not at present a goal; but any theory ought certainly to include every phenomenon of the rise of water in many or all trees, or show that those omitted are irrelevant.

Nothing about the rise of water strikes one who has seen it as more characteristic than its movement between the bubbles and the wall. When transpiration is at all active, the water must travel more than half of its course in this way. It must move very much more rapidly here than in places where it fills the entire lumen. Surely no theory can be complete which does not include a mechanical explanation of this passage of the bubbles.

Science has become so broad that no man can be proficient

in many of its branches, and as the field of labor is divided, we turn to the physicist for skill in the solution of such purely mechanical questions as this must be. But while as keen a worker as Schwendener can find no physical ground for even the existence of a flow past bubbles, we have only ourselves to rely on for an explanation. The soundness and thoroughness of physiology is usually measured by its nearness to physics and chemistry; but in the present state of physical knowledge on this point no theory can rest on it and be acceptable. The problem is distinctly outside of my province, and the experiments I have made on it were for the personal satisfaction of feeling a new field, without any thought of clearing it. I will speak of only two or three of them.

As stated before, Vesque's experiments in glass tubes are easy to repeat. If a coiled hair is pushed into a wet tube it straightens in part, but will hold up an obstruction such as a bit of copper slid down from above; and this will afford considerable opposition to the rise of a bubble let in from below; while the hair runs down the side of a tube from the water above to that below the bubble. With care, bubbles can sometimes be held in place by the hair alone, but not as certainly. I have found it convenient to set the tube, so fitted up, in a vessel of water on the top of a microscope; the focusing adjustments of the microscope served to elevate or lower the vessel. Measurements were with a cathetometer. The meniscus in the tube being well above the obstruction to the bubble, the vessel was slowly raised; the bubble was stationary, while the meniscus higher up slowly rose. Nothing else was to be expected; this need show only that the surface tension in the angles formed by the hair and the wall is sufficient to hold in the angle water which connects that above the bubble with that below it.

In a Jamin's chain, the bubbles moving with the water, and no water passing them, capillarity will hold the highest meniscus an indefinite height up in the tube. If Vesque's suggestion, that an atmosphere should lift in the wood a total of 10^m of water, exclusive of bubbles, is tenable, the height to which the highest

meniscus in a tube with a bubble past which water flows should be greater than in the same tube of unbroken water; but at first sight that looks unlikely. Some experiments seem, however, to indicate that it occurs. Thus, in a tube 1.3^{mm} in diameter (as nearly as I could measure), the height from the water outside to



the meniscus within was 23^{mm} ; with two bubbles in the tube the height was 23.9^{mm} ; after they were removed it was 23.1^{mm} . But in most instances I found the added height, after introducing a bubble or two, to be about 0.1^{mm} , which is too little to rely on as anything. Working with a tube obstructed by a hair alone, I have seen a bubble without any other provocation than an accidental jar, slide above the hair and make a Jamin's chain, and carry about 3^{mm} of water with it, so that the total water held up was 27.2^{mm} , instead of 24.2^{mm} . The energy to do this must have been furnished by the change in shape of the bubble. One more of these experiments will suffice. A piece of glass tubing was blown in the shape illustrated, and a bubble put in whose outline is shown by the curved lines at the two extremities of the figure; a hair passing around the bubble. Keeping the tube upright, it was subjected to an added pressure of 70^{cm} Hg. Within ten minutes the bubble was reduced one-half, as represented by the inner bounding lines; the immediate effect of compressing the bubble was to make the menisci at its two ends of different shape, and this difference caused water to flow up around the bubble.

While these experiments and others show the facility with which water can pass bubbles in vessels of uneven contour, they throw no light on the force which carries it around the bubbles in the tracheae; which is the question that needs answering. The ease of the movement, and its rapidity, and above all the pressure relations involved in the tracheae, are still quite in the dark. Since the water moves farthest and fastest here, it is greatly to be hoped that physicists will soon take a position with which we can get in touch.

Another problem hardly less in the dark than the physics of

the films of water around the bubbles is the resistance to be overcome by the movement of the transpiration stream. These two problems have much in common, but this one admits of a more conclusive experimental answer. According to most of the evidence we have, more energy is required to overcome this friction than in the actual lifting of the water. But this evidence is most noticeable for the discrepancies in it—cf., *e. g.* Janse with Strasburger or Sachs. In the most recent work on this subject, Curtiss (1901) concludes that the resistance offered by a stem to the flow of water at a fixed rate is not proportional to the length of stem. He also finds that the same force is required to overcome this resistance, whether it is applied as a pull or a push; which at most can be the case only within limits, because of the influence of the tension on the size of the bubbles. The rapidity of the movement of water can involve no inconvenient measure of friction, or the plant would provide for a slower current by allowing the conducting tissue a greater cross section. Instead of doing this the tree restricts its conducting area with tyloses, "gum," and changes in the wood itself, whose only known effect where they occur is to hinder the movement of water. In many trees, as in Robinia, the specialization is most decidedly toward the restriction of the transpiration stream to the youngest wood.

If it should be proven on the physical side that the water surface in contact with the bubble, in breaking half of the bonds that held it in the liquid state, had acquired some of the motility of a gas, the clearing up of the physics of the water surface would altogether alter our attitude in theory toward the friction problem. The idea that the surface of a liquid is more rigid than the interior, certainly arose from faulty experiments, but the truth of the matter is yet to be shown. If it should be found that the surface shared the properties of gases again in their relative indifferences to altitude, as Sachs suggests for the water of imbibition—and as is not at all impossible with a half-way vaporized surface—the calculation of the 10^m of water as the sum of the liquid indices alone will be justified at once. It is conceivable even that the elevation of water by surface tension

in the stem be active, the source of energy being the cooling of the stem, which would remove the 10^m limitation altogether. Arendt's observations, apparently of ascending currents maintained by capillarity, have not to my knowledge been corrected or explained. It is safe to assume that the plant does not work on a dangerously narrow margin, and 10^m of water in a tree 100^m high would leave a proportion of air for which we know no parallel. But it is idle to take advantage of what we do not know to spin out speculations.

This is not a satisfactory state in which to leave a subject. But it may still be regarded as something in "this most nebulous of subjects," as Darwin calls it, to have pointed out where our theories fail, and where our densest ignorance lies. The rise of water to make good the loss by transpiration is due to the pressure of the atmosphere, or to this and other forces cooperating with it and regulated by it. Much farther than this we cannot go until there is a physical explanation of the repeated botanical observation of the passage of water between bubble and wall.

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The absence of anything like a complete and easily accessible bibliography has been a difficulty in the preparation of this paper, which I have tried to spare for future work. Not only has there been a dearth of reference and credit to earlier work, and consequently a great deal of republication, but a surprising number of inaccurate references add to the difficulty. From this list of titles I have therefore omitted all those of works which I have been unable to consult and verify in person, excepting a few which it has seemed best to refer to on hearsay; these appear in brackets. In spite of this limitation, the bibliography will hardly be found glaringly incomplete. The few general texts listed contain matter on this subject which might appropriately have been published separately. The few purely physical works included here are to complete references in the body of this paper.

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SOME NOTES ON THE ECOLOGY OF THE DELAWARE COAST.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.
XL.

LAETITIA M. SNOW.

(WITH MAP AND TEN FIGURES)

IN July and August of 1901 the observations here recorded were made at Rehoboth Beach, Delaware, as a small addition to the increasing collection of data from the Atlantic seacoast. In sequence and nomenclature an attempt is made to harmonize these results with those obtained by Mr. Kearney¹ and Dr. Harshberger², on Ocracoke island and the New Jersey coast, respectively. The Britton and Brown nomenclature is used throughout, with the synonyms from Gray's *Manual*, where such occur, in parentheses. The list of plants does not claim to be complete, as the work was done during the summer months, and therefore the flowers of many species had disappeared, while other forms had not yet flowered, making identification difficult and at times impossible. Many forms were doubtless overlooked in the one or two visits which limited the opportunities for study in some parts of the field. The algae and fungi were not studied, while the lichens and mosses received the most superficial attention.

I. GEOGRAPHY.

The region studied extends from Cape Henlopen to a little over a mile south of Rehoboth, including a tract of land about six and a half miles long, by one-half to one mile in width, lying on the mainland, instead of on a fringing chain of islands, which is the usual condition along the Atlantic coast. The trend of the

¹ KEARNEY, T. H., The plant covering of Ocracoke island. Contrib. U. S. Nat. Herb. 5: 261-319. *figs.* 18. 1900.

² HARSHBERGER, J. W., An ecological study of the New Jersey strand flora. Proc. Acad. Philad. Oct. 1900.

coast line is almost due north and south, and the ocean currents come predominantly from the southeast.

II. PHYSIOGRAPHY.

A. Topography.—From the northeast end of Maine to the Florida peninsula the Atlantic coast is more or less fringed with islands, the shore lines of Delaware and Maryland being no

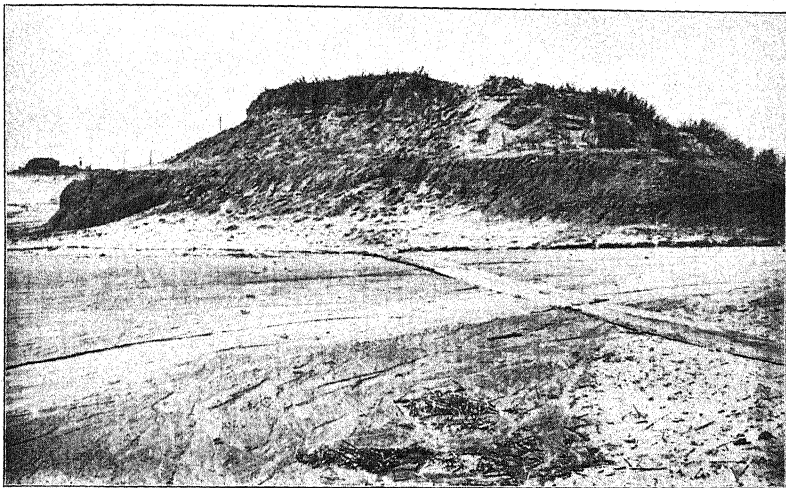


FIG. 1.—Shore south from Rehoboth, showing sandstone layer upon which is a dune; Douglas House at left, one mile to the south.

exception to the general rule. Here the bays and lagoons extend far into the mainland, usually surrounded by swampy tracts, broken up into sub-bays by low lying islands, and often connected by slowly flowing streams. In the course of time the lagoons and bays become filled up by sediment and plant remains. This process of filling up could be studied with great advantage in the Henlopen region, for all the stages from lakes through storm-flooded areas and swamps to the meadows are found, although the lagoon stage is past.

The sea beach is smooth and usually has a very gradual slope; the sand is fine and compact and is not easily drifted, therefore

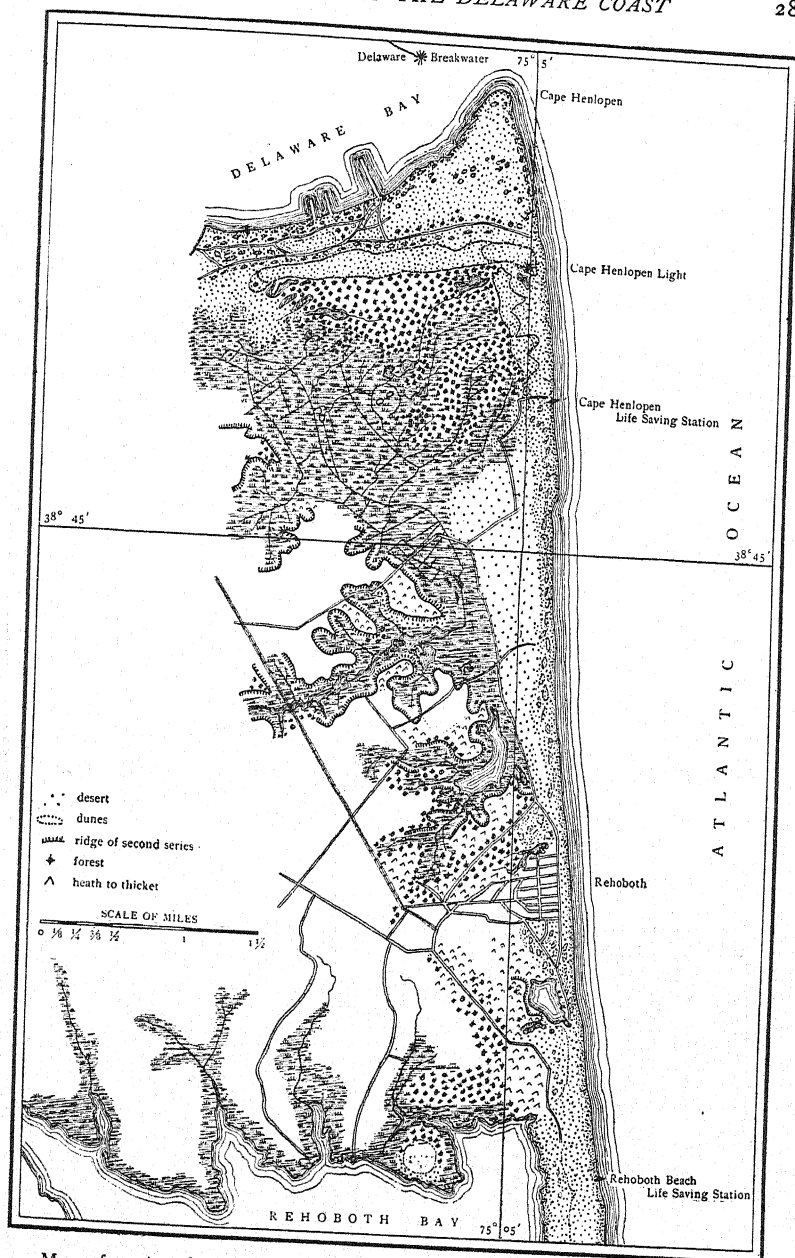
there is a tendency for low, more or less fixed dunes to form. Diagonally across the cape, however, is a large active dune, which by comparison with the 75-foot lighthouse seemed to be about 80-90 feet high. To the southwest of this are several smaller active dunes, becoming lower and more stable toward the south. A row of small dunes, somewhat fixed, edge the beach around the cape, enclosing a region of swamps, meadows, lakes, and low dunes. South along the beach extends a line of dunes, with a second series back from it, the distance between the two varying greatly at different places. Meadows, swamps, lakes, and small dunes occupy this space.

The second series extends in a very irregular line across the cape (see map), and since these dunes must have been blown in from the coast it is natural to suppose that the coast at one time was parallel to them (S.E.-N.W.), instead of projecting to the northeast as now. The supposition that Cape Henlopen has grown out from a S.E.-N.W. coast, and is still growing, is supported also by the formation of hooks on the western shore by the southeast ocean currents. Such cape and hook formation is described and figured by Gerhardt³ from the coast of Europe.

Back of the second series of dunes a plain slopes to the thicket and forest, broken in places by meadows and small dunes, and interrupted by fields. This plain, for want of a better name, I have called a "heath;" physiographically it corresponds with that type, although it is not characterized by the typical plants.

B. Soil. — 1. CHARACTER. — The soil is predominantly sandy throughout, usually nearly to the surface, where a thin layer of humus appears in the moister regions. The beach is nearly pure sand, with a few patches of clay in hollows, where it is deposited by the wash of storms. From Rehoboth for about a mile south there crops out along the beach a deposit of sandstone. This being much more resistant than pure sand stands out in step-like structures, upon which dunes are usually superposed (*fig. 1*). In

³ GERHARDT, PAUL, *Handbuch d. Deutsch. Dunenbaues*. Berlin. 1900. pp. 43-46, 61-63.



Map of region from Cape Henlopen to Rehoboth bay. Adapted from Coast Chart no. 127, U. S. Coast and Geodetic survey.

several places, however, the dunes have either not formed there, or have passed back, leaving a golden brown slab of hard material. On the beach pieces of iron ore were found, washed from an undetermined source. Back in the dune region are tracts of land almost totally destitute of vegetation (*fig. 2*). These desert spaces are rain-washed in times of storm, and hold water for some little time, the water washing into the depression

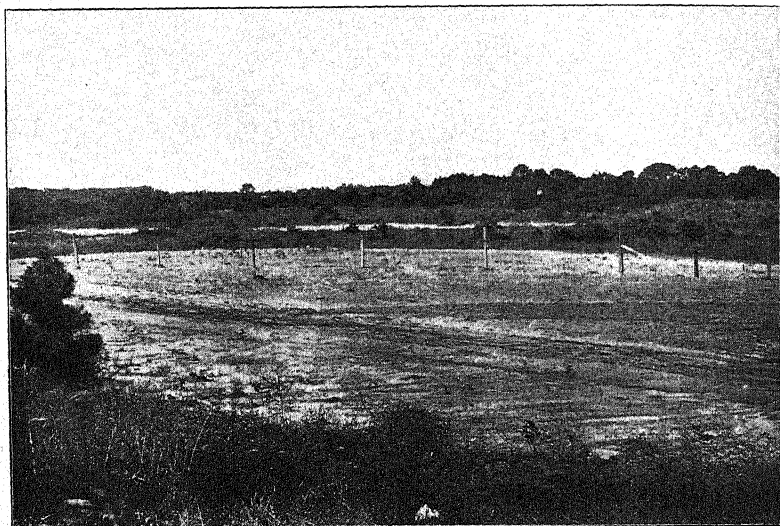


FIG. 2.—Bare space between dune series; second series immediately beyond, on crest of which a thicket is forming; forest beyond.

from a higher region, and then evaporating, covering the ground with a deposit of sand and clay, which becomes baked in the hot sun. The ground is so unfavorable for the existence of plants, that very little vegetation is found here. In the swamps and meadows a layer of humus covers the sand to a greater or less depth, according to the character of the vegetation, the exposure, and the length of time of deposition.

2. SOIL WATER.—Water level is very near the surface, in most places only a slight depression being needed for the development of a swamp. The water furnished by pumps in the vil-

lage is strongly impregnated with iron, showing that a stratum of ferruginous material underlies at least part of the region.

III. CLIMATOLOGY.

A. Rainfall.— Besides lacking state geological and topographical surveys, Delaware has no Weather Bureau station, and therefore the statements concerning the climate must be very general. From the Rainfall Division of the U. S. Weather Bulletin, 1897, the following facts were obtained. The mean annual precipitation is 40–50 inches in the Middle Atlantic states. The distribution here is more uniform than in any other part of the country, 20–25 inches being the usual amount in the growing season (April–September), the least recorded for this period being 10–15 inches.

B. Heat and light.— During the two months spent at Rehoboth a very imperfect record of temperature and direction of the wind was kept, and in the absence of accurate reports the results will be used for comparison. The temperature figures for the New Jersey and North Carolina stations were kindly furnished by the U. S. Weather Bureau, the mean temperature for July and August, 1901, being as follows:

	July	August		July	August
Atlantic City, N. J.	- 75	74	Cape May, N. J.	- 75.6	73
Rehoboth, Del.	- 77.7	78.4	Cape Hatteras, N. C.	78.9	79.5

Even on cloudy days the light on the coast is more intense than inland, on account of the reflection from the sand surface, while on bright days it is almost blinding. The amount of heat radiated by the sand is considerable, and taken in connection with the reflected light must necessarily have great influence upon the flora, only those plants appearing that are able to adapt themselves to these severe conditions.

C. Wind.— The direction of the wind, as well as its force, is very important with reference to the shape and size of the dunes. For the two months during which these observations were made the prevailing wind was southwest, alternating with northeast during July, and becoming more variable in August. No observations being made during the other months, no conclusions as to

the prevailing wind for the year can be drawn. The oaks and cedars bend away from the shore, as is usual, their outer branches suffering from the salt-laden wind, while the more protected limbs grow fairly well, thus producing a one-sided plant. The prevailing wind is not necessarily the dune-forming wind. For that other factors must be considered: the strength of the wind, the sweep over an expanse of surface, the absence of obstacles in the path, and lastly the angle at which it meets the shore. At Cape Henlopen the northeast wind is probably the strongest, having a sweep over the mouth of Delaware bay, and meeting the shore at a large angle; hence the dune is moving across country southwest. Farther down the coast the northeast wind meets the shore at a small angle, while the lighter east wind strikes perpendicularly. In this case the dune movement depends upon which factor is the stronger. The dunes here have become practically fixed, but what little movement there is appears to be directly west.

IV. PLANT FORMATIONS.

As a matter of convenience in harmonizing the two regions, the order used by Dr. Harshberger is adopted here so far as possible. Although adjacent situations, the conditions differ somewhat, because the region from Henlopen to Rehoboth bay is at a higher stage of physiographic development than the New Jersey beaches.

A. Treeless open.—I. BEACH FORMATION.—(a) *Lower beach.*—For reasons pointed out by Dr. Cowles⁴ and Dr. Harshberger⁵, the lower beach is incapable of supporting vegetation. We find it composed of bare sand, extending back, usually in a gentle slope, to the line of summer driftwood.

(b) *Middle beach.*—(i) *Succulent zone.*—At Rehoboth and northward the summer tides wash up to a ridge of driftwood and débris, where the loose sand first gathers, seeds rest and

⁴COWLES, H. C., The ecological relations of the vegetation on the sand dunes of Lake Michigan. BOT. GAZ. 27: 114-185. 1899.

⁵Loc. cit. 639.

germinate, and such plants as *Cakile* sp., *Salsola Kali*, *Xanthium* sp., and *Atriplex arenaria* are found. Here also we find tufts of *Ammophila arenaria* (*A. arundinacea*), although it is not a character plant. This succulent zone is in some places confined to the ridge of débris around the bases of the low dunes, in others it extends much further back. It may reach many feet inland, to the foot of the higher dunes, or may even form channels by which the sea enters inland lakes in times of storm. The name of the zone indicates the structure of two of the characteristic species, *Cakile* and *Salsola*, and of the rarer *Atriplex*.

(ii) Low *Ammophila* dune zone.—From the line of summer driftwood to that of winter driftwood has been called by Dr. Cowles⁶ "middle beach," while above the winter drift line the "upper beach" extends to the foot of the dunes. Here conditions are different. The winter drift line usually lies at the foot of the higher dunes, although logs are sometimes found on the low dunes. Hence there is no "upper beach" corresponding to that on the Lake Michigan strand, but what corresponds to the "middle beach" is more or less distinctly divided into two zones, which are designated here as "succulent zone" and "low *Ammophila*-dune zone." As the name indicates, the upper belt is characterized by low dunes held by *Ammophila arenaria*, in association with *Panicum amarum* and *Cenchrus tribuloides*, while scattered mats of *Euphorbia polygonifolia* and bunches of *Oenothera humifusa* occur. *Xanthium* comes up from the lower zone in places, and *Leptilon canadense* (*Erigeron canadensis*) wanders to some extent from the higher dunes. From the fact that the winter drift line lies back of these dunes, it seems probable that they are of annual formation. This question was not settled definitely, but in July they appeared to be rather large and firm for spring planting. North of Rehoboth the succulent zone is very narrow or entirely wanting. The beach is wide and bare and slopes to the first ridge of dunes, the low *Ammophila*-dune zone being omitted, or no distinction appearing between it and the next belt. At the Cape the same conditions obtain, the

⁶ *Loc. cit.* 115.

lighthouse dune coming down, a bare, loose slope, to the beach. South of this is a hollow, formed by active dunes, and in which lies a swamp. Just in front of this swamp are the remains of the only low *Ammophila* dunes in this part of the region.

2. DUNES.—(a) *Outer series*.—South of Rehoboth this outer series is practically fixed. The sea face is exposed to storms from the sea, and is sharply eroded. North of Rehoboth this series is more active, being formed of loose sand partially held by *Ammophila*, the activity increasing until the lighthouse dune

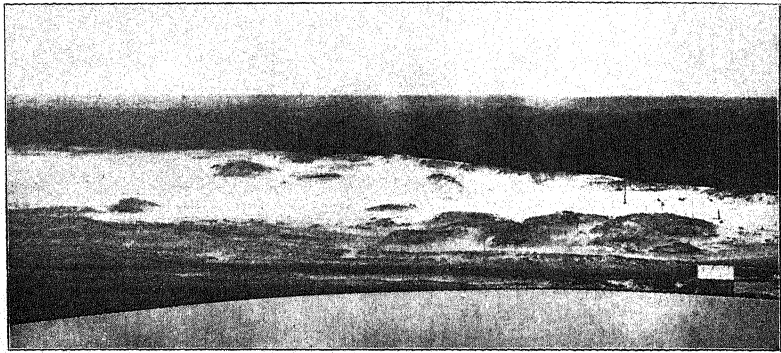


FIG. 3.—Southwest from lighthouse; lighthouse dune in foreground; swampy hollow at center; active dunes ("pine graveyards"), beyond which is a pine forest.

forms the climax. In this region they have a rounded form due to their activity. For most of the distance from Rehoboth to the Cape this series varies in height from 6–10 feet, getting higher to the north, where it culminates in the 80–90 feet lighthouse dune. In places it slopes from its crest into a heath, although it is usually followed by a dune complex or swampy meadow. Just south of the lighthouse dune lies the previously mentioned semicircle of active dunes enclosing a swamp. Other dunes stretch in a S.E.-N.W. direction, showing a northeast wind action. On the windward slopes of these dunes are several "pine graveyards"⁷ (fig. 3), the remains of the forest over which the dunes are now passing. A little further south, at the

⁷ COWLES, *loc. cit.* 298.

life-saving station (see map), the dunes have retreated quite a distance, and the place now occupied by active dunes was once a line of fixed pine dunes, for the active crest shows knobs still held by pines, and the dead trunks falling on the windward side. Coming from the beach over the waste of drifting sand, back of the life-saving station, and climbing to the crest of this active dune, one is startled by the contrast formed by the view towards the west with that on the windward side of the ridge. The dune is sweeping into a marshy meadow, apparently stretching for

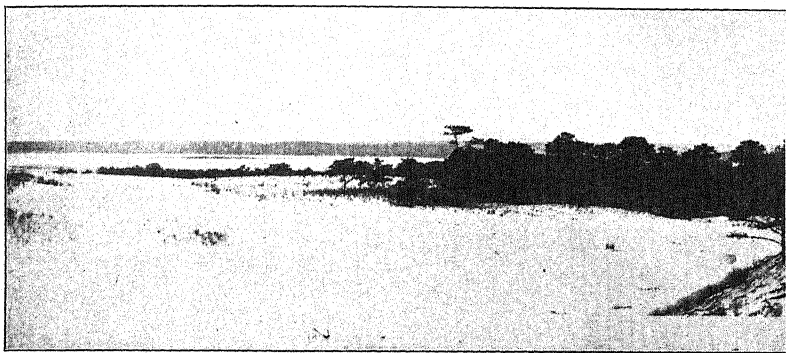


FIG. 4.—Southwest from life-saving station dune; extreme right, rejuvenated face of old pine dune appearing again at center; active dunes to left; desert waste in middle distance showing a grass island.

miles to the southwest, and cut up towards the coast by ridges, upon which stand tall pines. One ridge is seen running nearly perpendicular to the active dune, and others at smaller angles. *Fig. 4* shows the rejuvenated face of one of these ridges. Between this rejuvenated dune and the shore just south of the life-saving station lies an active dune complex, containing meadows and swamps. Further to the south the complex spreads out and borders a broad level desert reach (seen in the distance in *fig. 4*, partially covered by water), the outer line of dunes following the shore, the inner ridge swinging off to the southwest. As the outer series north of Rehoboth is the frontal ridge, it has the sloping sea face sparsely covered with *Ammophila*, as is the case

with the low frontal dunes south of the village. South, however, the face of the first series of higher dunes is eroded, more probably on account of the fixed condition of the dunes than from any protection which the frontal line offers. This eroded surface has very little vegetation, some few plants from the top having fallen and taken root. In places where the erosion is not so great, this slope is characterized by *Ammophila*, *Euphorbia polygonifolia*, and *Leptilon canadense*. Over the edge, on the more protected slope also appear *Cassia nictitans*, *Oenothera humifusa*, *Strophostyles helvola* (*S. angulosa*), *Panicum amarum*, *Ionactis linariifolius* (*Aster linariifolius*), *Rumex* sp., etc., grading into heath forms, as *Lechea minor* (*L. thymifolia*), *Baptisia tinctoria*, *Myrica cerifera*, *Baccharis halmifolia*, *Rhus copallina*, *Diospyros virginiana*, followed by clumps of *Pinus rigida*, *Juniperus virginiana*, and *Quercus digitata* (*Q. falcata*). This first series borders the cape in a practically complete line, openings allowing the sea in times of storm to wash into the depressed area within. This region is covered mostly by swampy meadows (the dominant form being apparently *Spartina patens*) with open water in places. In this extended swampy area rise small rounded or elongated dunes, the higher ones topped by pines (*Pinus rigida*). In one clump of pines, occupying a depression surrounded by dunes, an undergrowth of *Myrica cerifera* and cranberry indicated a pine swamp flora. Such swamps doubtless occupy similar situations in the depressed area.

(b) *Hudsonia complex*.—Back of the protecting ridge of the first series lies a region of general depression in which at certain places low dunes extend in all directions, forming a complex, and held mainly by *Hudsonia tomentosa*. In places the formation is almost pure, in others various forms appear. These dunes are rounded in form, and about a foot or two in height, corresponding to the habit of the plant holding them. Swamps and meadows extend among these dunes, produced in most cases by the flooding in of the sea during winter storms, the ground remaining wet for most of the year. This complex is best seen south of Rehoboth, between the sea and Silver lake.

(c) *Swamps and meadows*.—The swamps found between the two series of dunes are undrained for at least part of the year, the history of Silver lake being a good example of what probably takes place in the majority of lakes and swamps of this region. During winter storms the sea comes in through openings in the outer ridge and floods the lake until its boundaries extend around the low dunes in its vicinity. During the summer months the lake margin retreats, leaving wet soil, and sometimes water standing in the depressions. This drying process nearly converts Silver lake itself into a swamp, very little open water being visible, an increase only occurring at times of unusually high storm tides and during showers. The first event occurs but rarely, and the amount contributed by the second method is not sufficient to supply the loss occasioned by evaporation during the hot dry days.

Around the edge of Silver lake grows *Scirpus americanus* (*S. pungens*), the growth being much more luxuriant at the north end, where the water is fresh. In places also occur *Cyperus ferox*, *C. diandrus elongatus*, and *C. Nuttallii*. At the south end of the lake, where the main entrance from the sea lies, were found such strand forms as *Polygonum maritimum*, *Dondia americana* (*Suaeda linearis*), and *Atriplex hastata* (*A. patulum hastatum*); while at the northern end the formations show a tendency toward fresh-water forms, passing from a swamp to a wet meadow and thence to drier conditions. Here we find such forms as *Scirpus americanus*, *Hydrocotyle umbellata*, *Hypericum canadense*, *Cassia nictitans*, *Pluchea camphorata*, *Linum virginianum*, *Linaria canadensis*, *Fuirena squarrosa*, *Xyris flexuosa*, becoming gradually replaced by *Spartina patens* (*S. juncea*), *Ambrosia artemisiaefolia*, *Solidago sempervirens*, *Erechtites hieracifolia*, *Gnaphalium purpureum*, *Erigeron ramosus* (*E. strigosus*), *Carex silicea* (*C. straminea moniliformis*), *Juncus tenuis*, *Fimbristylis castanea*, and *Scirpus subterminalis terrestris*. *Xanthium* sp., *Mollugo verticillata*, and other more xerophytic forms appear on low elevations and toward the dunes.

West of the lake lies a small meadow worthy of mention because it holds a plant assemblage not seen elsewhere, although

some forms present are the usual meadow species. Following the belt of *Scirpus americanus* and *Spartina patens* which borders the water of a small lily pond west of Silver lake is an association of *Strophostyles umbellata* (*S. peduncularis*), *Diodia virginiana*, and *Cyperus cylindricus*. Higher up appear *Hieracium Gronovii*, *Asclepias incarnata*, *Galium pilosum*, *Gnaphalium purpureum*, *Solidago sempervirens*, *Festuca rubra*, *Panicum amarum*, *P. sphaerocarpon*, and *Sieglingia seslerioides* (*Triodia cuprea*), out of which assemblage rise the stalks of *Kosteletzkya virginica*. One place a little more depressed supports *Iris* sp., *Achillea Millefolium*, *Daucus Carota*, *Rhexia Mariana*, *Lactuca canadensis*, *Prunella vulgaris* (*Brunella vulgaris*), *Salvia urticifolia*, and *Viola sagittata*. *Eupatorium hyssopifolium* and *Solidago canadensis* occur also, showing a tendency toward drier conditions.

That Silver lake extended in former years much beyond its present boundaries may be supposed from at least three things. First, by comparison with the chart of the Coast Survey no. 127, from which the map given has been copied, with what corrections appeared to be needed; second, from the presence around it of meadows, whose hydrophytic forms are being replaced by mesophytic species; and third, the presence of a clump of *Iris* on the east shore of the lake, but no longer in swamp conditions, being now on top of a flat dune.

The Hudsonia complex, back of the first line of dunes, and protected from the ocean winds, is subjected on its western edge to winds sweeping over the lake and the plain beyond. The dunes here show a windward slope covered with roots and débris of dead plants, uprooted and destroyed by the wind action (fig. 5). Toward the south end of the lake these dunes become low and are occupied chiefly by *Spartina patens*.

Across the lake, on its western border, rises the second series of dunes, bending round the meadow described above, and including in the bend a thicket of sumac (*Rhus copallina*), wax berry (*Myrica cerifera*), pines, cedars, oaks, and *Baccharis halmifolia*. Northward the depression between the two series is broad, and we find many mesophytic areas, probably the remains

of former swamps. Southward the depression narrows and for some distance is occupied by a road. Farther south it broadens out into a bare rain-washed area of hard baked soil with few plants, such as *Panicum sphaerocarpon*, *Antennaria plantaginifolia*, *Ionactis linariifolius*, *Diodia teres*, *Plantago aristata*, etc. This bare space passes seaward into a wet meadow which in turn slopes toward the dunes, *Spartina patens* replacing the meadow

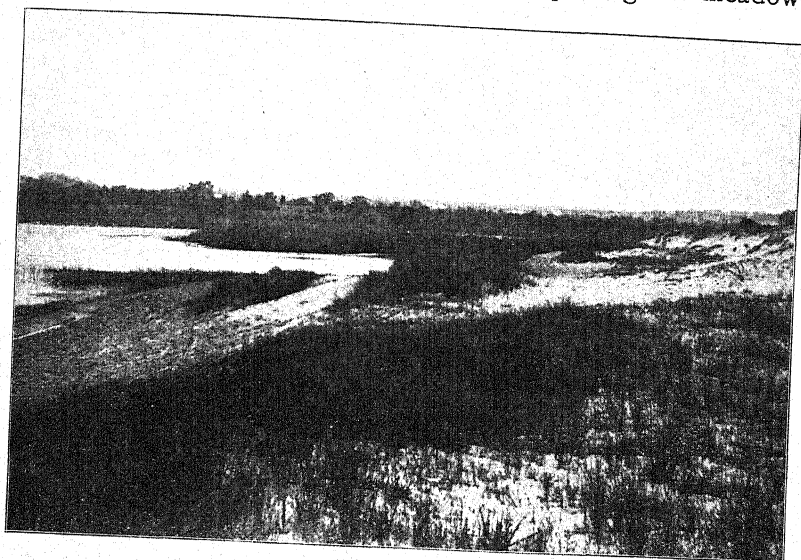


FIG. 5.—East shore of Silver lake, showing at extreme right windward faces of dunes moving eastward; the swampy character of shore of the meadow extending northward.

forms, among which may be mentioned *Senecio tomentosus*, *Hieracium Gronovii*, *Gnaphalium purpureum*, *Viola sagittata*, and giving place to *Ammophila* toward the crest of the dunes, which here slope directly to the beach, no low dunes being present.

North of Rehoboth the two series open out in a V, near the apex of which lie Hudsonia dunes and swamps, one of which is a pine swamp. In this was found the typical pine swamp flora, *Osmunda regalis*, *Dryopteris Thelypteris* (*Aspidium Thelypteris*), *Oxycoccus macrocarpus* (*Vaccinium macrocarpon*), with *Xyris flexu-*

osa, *Rhexia virginica*, *Myrica cerifera*, *Rhus copallina*, and *Smilax rotundifolia*. No *Sphagnum* was found, however, during the one visit paid to this swamp. In another swamp in this region appeared an association of *Polytrichum* sp. and *Lycopodium inundatum*; while in still another *Iris* sp., *Hibiscus Moscheutos*, *Senecio tomentosus*, and *Viola sagittata* were grouped together.

On the Hudsonia dunes between the two series we find,

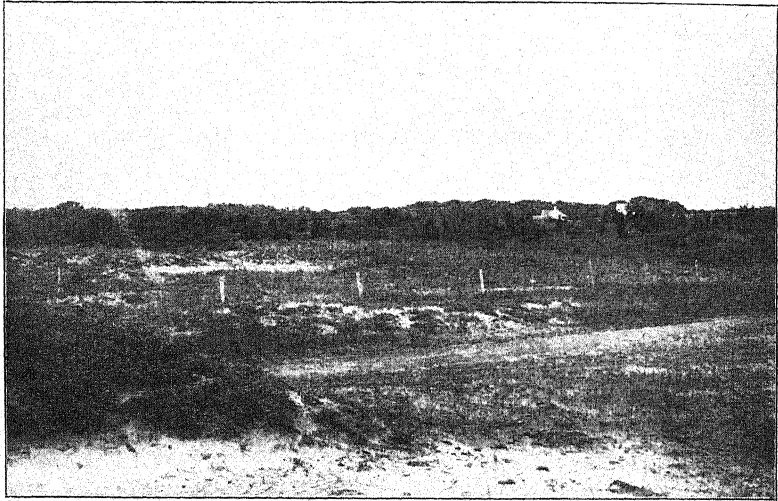


FIG. 6.—Hudsonia complex south of Rehoboth, a nearly pure formation; heath character is not developed; Hudsonia dune in left foreground.

besides *Hudsonia tomentosa*, *Lespedeza frutescens* (*L. reticulata*), *L. capitata*, *Meibomia obtusa* (*Desmodium ciliare*), *Cassia chamaecrista*, *Crotalaria sagittalis*, *Strophostyles helvola*, *Solidago canadensis*, *Euthamia caroliniana* (*Solidago tenuifolia*), *Myrica cerifera*, *Pinus rigida*, *P. virginiana* (*P. inops*), and *Juniperus virginiana*, which, with some bushes of *Gaylussacia resinosa*, *Vaccinium corymbosum*, *V. atrococcum* (*V. corymbosum atrococcum*), and *Oxycoccus erythrocarpus* (*V. erythrocarpon*) give the region a heath-like appearance (figs. 6, 7).

Farther north extends a low, flat meadow, swampy in places,

and containing lily ponds (fig. 8). Here were found such character plants as *Spartina patens*, *Hibiscus Moscheutos*, *Solidago sempervirens*, *Juncus scirpoides*, *J. tenuis*, *Sabbatia stellaris*, *Polygonum hydropiperoides*, *Xyris flexuosa*, etc., *Andropogon virginicus* and *Carex silicea* occupying a little higher ground. Some portions of this swampy meadow are undoubtedly under water during the winter

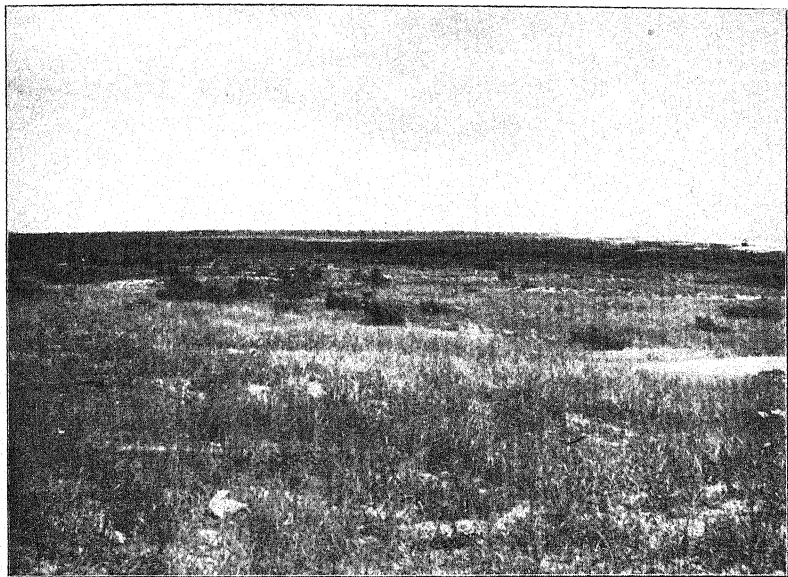


FIG. 7.—Hudsonia complex north of Rehoboth, with heath-like character somewhat developed; looking toward Henlopen light to northeast from the board walk; coast with first series of dunes shows in right background; clumps of *Myrica*, oaks, pines, with *Hudsonia* dunes in center background.

storms, the sea coming in through openings in the dunes of the first series.

This meadow area stops rather abruptly on its northern edge, at the desert-like expanse referred to above, which extends nearly two and a half miles north and south, by five-eighths of a mile at its widest point. Several inlets give an opportunity for the sea to flood this region during storms; in fact, the whole sandy area is reported to be covered with water "three foot deep" in winter,

but during the summer a part of it at least was dry. The process of filling up and reclamation seems to be progressing from the meadow, where adventurous plants are creeping out over the waste. This end must be higher than the northern end, for during a part of the summer the water remained in the latter. Several low dunes lie scattered like islands on this desert, their



FIG. 8.—North from board walk on second series, a continuation to left of *fig. 7*; meadow showing in right background with a lake at left; the continuation of the second series at left.

flora, consisting apparently of grasses and sedges, making a weak attempt to spread over the sand. Why has not this region a swamp flora? Swamps are frequent in the inlets, therefore lack of water is apparently not the cause. Only two trips were taken over this desert; they were excursions, therefore careful investigation was impossible. It gave promise, however, of yielding more interesting results.

(*d*) *Second series*.—This series has been mentioned so frequently in the discussion of other regions that little needs be

said here. *Ammophila* characterizes the crest, associating with heath forms as the plain slopes toward the west. Just north of Rehoboth is a good example of this condition. Here scant *Ammophila* growth is accompanied by *Lespedeza procumbens*, *Sarothra gentianoides* (*Hypericum nudicaule*), *Lespedeza capitata*, *Helianthemum canadense*, and *Pinus rigida* just over the crest; while four clumps of *Panicum virgatum* stand out on the windward side among the scant vegetation creeping up from the Hudsonia complex.

3. HEATH.—Although small portions of heath occur in many places on the lee side of the first series of dunes, the heath proper must be considered as starting from the second series and extending back to the forest. Its chief characteristic appears to be its large number of species of varied distribution, with very few that stand out as character forms, even the most common plants not being characteristic of all parts of the heath. Just south of Rehoboth occurs the most typical piece of this formation (fig. 9), being less interrupted by roads, cultivated fields, etc., than elsewhere, consequently most of the forms mentioned were collected in this region. It is a wilderness of *Baptisia tinctoria* and blackberries (*Rubus villosus*, *R. cuneifolius*, *R. canadensis*), with occasionally almost meadow-like growths of *Ammophila*. In clumps or singly rise cedars (*Juniperus virginiana*), persimmons (*Diospyros virginiana*), pines (*Pinus virginiana*, *P. rigida*), oaks (*Quercus digitata*), *Prunus maritima*, *P. pennsylvanica*, *Myrica cerifera*, *Rhus copallina*, and *Helianthemum canadense*, with an occasional *Sassafras sassafras* (*S. officinale*). A bush or two of *Rosa humilis* appeared at two points, and holly (*Ilex opaca*) at only one. Among the herbaceous dicotyledons from rare to frequent were observed *Solidago juncea*, *S. canadensis*, *Eupatorium album*, *E. hyssopifolium*, *Erigeron ramosus*, *Leptilon canadense*, *Aster ericoides*, *Gnaphalium obtusifolium* (*G. polycephalum*), *Achillea Millefolium*, *Lactuca canadensis*, *Hieracium Gronovii*, *Ascyrum hypericoides*, *Sarothra gentianoides*, *Asclepias tuberosa*, *Linaria canadensis*, *Trichostema dichotomum*, *Meibomia arenicola* (*Desmodium lineatum*), *M. obtusa* (*D. ciliare*), *Rumex* sp., and in

some places *Hudsonia tomentosa* forming small, almost pure formations. Of the monocotyledons, next in importance to *Ammophila* comes *Andropogon virginicus*, becoming more abundant as *Ammophila* decreases toward the west. With it are also associated in different places (besides various dicotyledons) *Agrostis alba*, *A. hyemalis* (*A. scabra*), *Eragrostis pectinacea*, *Pani-*

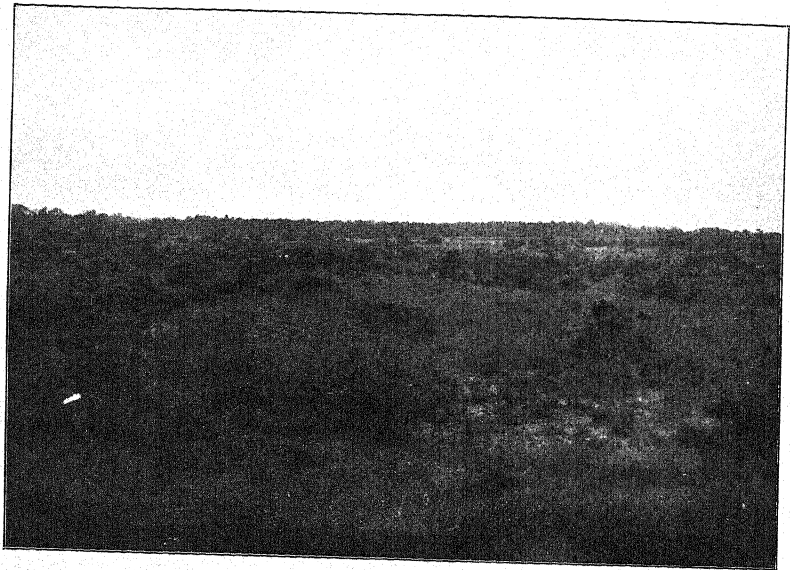


FIG. 9.—Heath south of Rehoboth, looking nearly due west.

cum sphaerocarpon, *P. viscidum* (*P. scoparium*), and *Poa compressa*; *Paspalum setaceum* occurring rarely. In many places there appeared a carpet of lichens and mosses, the most prominent of which were "reindeer moss" (*Cladonia rangiferina*) and *Ceratonodon purpurea*, while Geasters occurred frequently in such situations. Lianas were almost entirely absent, *Parthenocissus quinquefolia* (*Ampelopsis quinquefolia*) being found at only three points, *Vitis aestivalis* on one dune summit, while *Smilax rotundifolia* occurred only in the pine swamp described.

At one point south of Rehoboth, a single dune rising from a bare space has developed upon its summit a heath flora, com-

posed of plants which occur elsewhere only rarely or not at all. Among a thicket of blackberries, indigo, and cedars was found the only plant of *Crataegus coccinea* (*C. pruinosa* Wendl.) appearing in the whole region. *Vitis aestivalis* and *Festuca octoflora* (*F. tenella*) were also found here only. Besides these, there appeared the usual heath forms: *Andropogon*, *Lechea*, *Meibomia obtusa*, *Lespedeza capitata*, *Hudsonia*, *Panicum sphaerocarpon*, with *Solidago sempervirens*, *Galium pilosum*, and *Poa pratensis*. By roadsides and near dwellings were found such plants as *Plantago lanceolata*, *Poa pratensis*, *Daucus Carota*, *Achillea Millefolium*, *Lepidium virginicum*, *Chrysanthemum Leucanthemum*, etc., while one clump of *Opuntia* sp. occurred back of a cottage at the extreme end of the village.

B. Wooded region.—1. THICKET FORMATION.—This formation was merely glanced at in one situation, therefore no general idea can be formed of its character. At this one point were found *Aronia arbutifolia* (*Pyrus arbutifolia*), *Malus malus* (*Pyrus malus*) from cultivation, *Seriocarpus astroides* (*S. conyzoides*), *Ilex glabra*, *I. opaca*, *Vaccinium corymbosum*, *V. arboreum*, *Juniperus virginiana*, and *Pinus rigida*. With these forms occur many heath species, for this formation grades on the one hand into the heath and on the other into the pine forest.

2. FOREST FORMATION.—About a mile west of the village the oak woods appear as a belt back of the pine region. Here appears *Quercus digitata*, which gives place to *Q. alba*, *Q. coccinea*, and *Q. nigra*, with an occasional *Hicoria ovata* (*Carya ovata*). In the oak woods a canal has been started towards Rehoboth bay, but it is now abandoned, forming a deep cut partly filled with water and supporting a swamp flora. The excavation has broken up the fixed condition of the soil, and just west of the canal, possibly composed of the excavated sand, rises a fair-sized dune (fig. 10). At this distance from the coast the northeast and southwest winds seem to be about equal, and the dune is "going both ways," a process resulting in a flattening of the crest. It is of rather loose sand, with very little vegetation; grasses and occasionally a composite or sedge were all that gave it character.

Back in the country, pine and oak belts alternate for some distance, but no attempt to study this region was made.

V. CONCLUSIONS.

Dr. Harshberger⁸ and Mr. Kearney^{9, 10} have given sufficiently extended discussions of the geographical affinities of the floras of New Jersey, Ocracoke, and Virginia, to render any additional

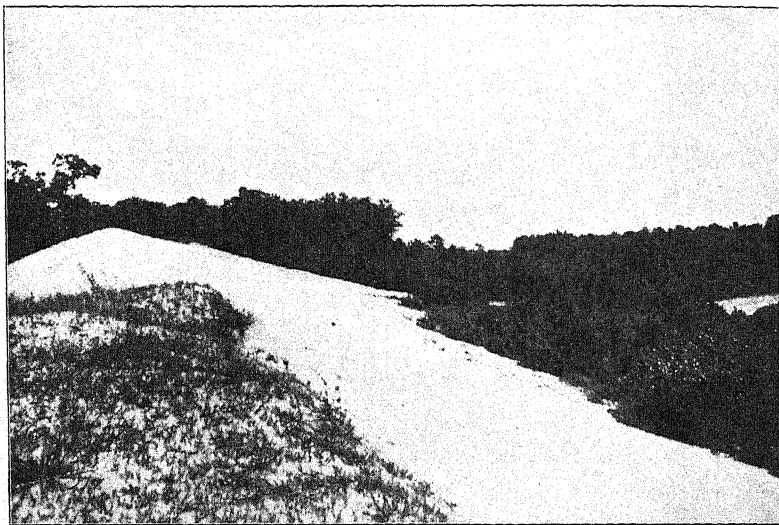


FIG. 10.—Dune west of Rehoboth.

remarks unnecessary, only a few words being required to place these observations in line. The conditions on the Delaware strand are in general similar to the conditions on the whole Atlantic coast, the Gulf,^{11, 12} and Lake Michigan shores. The beach is characterized by a succulent zone, in which *Cakile* and

⁸ *Loc. cit.*, 658.

⁹ The plant covering of Ocracoke island, p. 312.

¹⁰ Report on a botanical survey of the Dismal Swamp region, p. 458. *Contrib. U. S. Nat. Herb.* 5: 321-585. 1901.

¹¹ LLOYD, F. E. and TRACY, S. M., The insular flora of Mississippi and Louisiana. *Bull. Torr. Bot. Club* 28: 61-101. *pls.* 8-11. 1901.

¹² WEBBER, H. J., Notes on the strand flora of Florida. *Science*, N. S. 8: 658. 1898.

Salsola almost invariably occur, although their accompanying forms, *Xanthium* and *Atriplex*, are not so widely distributed. On the dunes the character plant, *Ammophila*, is of northern distribution, and is not found south of Chesapeake bay, but is abundant on the Michigan coast. Of its associates, *Euphorbia polygonifolia*, *Leptilon canadense*, and *Cenchrus tribuloides* are widely distributed, *Panicum amarum* is absent from the lake flora, and *Oenothera humifusa* extends along the Atlantic coast only to New Jersey.

Back of the first line of dunes, the combination of low dunes, swamps, and meadows offers a wide choice of habitat for plants, and we find many plants of wide range. The dune-holder *Hudsonia tomentosa* is a plant of northern distribution, Maryland being its southern limit, but it has a western range. Associated with *Hudsonia*, such forms as *Myrica cerifera* and *Baccharis halmifolia* are distributed along the Atlantic coast, but neither is found on Lake Michigan. Many grasses, sedges, and legumes are widely spread and need not be taken into consideration. *Strophostyles helvola*, very characteristic in Delaware, is mentioned only in the reports from New Jersey and Mississippi. *Spartina patens* shows a preference for salt conditions, appearing all along the sea and gulf strand, but not forming a part of the lake flora. Among the plants characteristic of the heath we find some widely distributed grasses and composites, although *Juniperus virginiana* stands out preeminently the most widely spread. *Quercus digitata* and *Diospyros virginiana* extend from Rhode Island and New York to the gulf; *Rhus copallina* is mentioned only in the New Jersey and Virginia floras; while the widely spread *Rhus radicans* (*R. Toxicodendron*) was found at Rehoboth in only one situation in the woods. Of the pines, *Pinus Taeda*, reaching (according to Britton and Brown) its northern limit in Delaware, was not found, although it is reported at Cape May, the peculiar conditions there obtaining accounting for its presence.¹³ *Pinus rigida* and *P. virginiana*, however, extend north and south of this region.

¹³ HARSHBERGER, 632.

A surprising lack of lianas was observed in the Delaware region, *Parthenocissus* occurring occasionally, and *Vitis aestivalis* and *Smilax rotundifolia* appearing in one situation, while "trumpet creeper" was collected in the surrounding country. This scarcity of climbers is in striking contrast to the condition described for other strand regions.

The pine swamp flora (*Osmunda*, *Dryopteris*, *Oxycoccus*, etc.) is composed of the usual undrained swamp forms, but no *Sphagnum* was found, and apparently the same is true of New Jersey, although one or two species are reported for Virginia.¹⁴

The similarity of strand conditions is therefore shown by the similarity of floras, for regardless of a wide difference in temperature there is a striking resemblance between the lists of forms found in New Jersey and Delaware and those reported for Mississippi, Louisiana, and Florida, while in spite of the fresh water condition on Lake Michigan the occurrence there of many genera and species which also inhabit the ocean strand bears evidence of common factors in the environment. These seem to be the excessive light and heat and strong wind-action of the sandy regions, the last being probably the most important element. In addition, the power of a large body of water in equalizing temperature explains in part the presence of many forms on the New Jersey, Delaware, and the Gulf coasts.

I wish here to express my thanks to Dr. C. F. Millspaugh of the Field Columbian Museum, Mrs. Agnes Chase of Chicago, Dr. J. N. Rose of the National Museum, and Dr. J. W. Harshberger of the University of Pennsylvania, for their kind assistance in identification; and I wish also to acknowledge my indebtedness to Dr. H. C. Cowles and Professor John M. Coulter for valuable criticism and suggestions.

THE UNIVERSITY OF CHICAGO.

¹⁴ KEARNEY, Dismal Swamp 428

BRIEFER ARTICLES.

A NEW WESTERN CAMASSIA.

IN 1880 Mr. William N. Suksdorf collected in Falcon valley, Washington, specimens of *Camassia*, which were sent to the Gray Herbarium for identification. One of these specimens was correctly referred by the late Sereno Watson to *Camassia esculenta* Lindl.; the other, an incomplete specimen, and a duplicate collected in 1883, were referred to *C. Leichtlinii* Watson. Since that time the same collector has carefully watched the growth of these plants in the field, and has even brought several species of the genus into garden cultivation for the purpose of ascertaining their true systematic position and relationship. Full notes and additional complete specimens have been forwarded the writer by Mr. Suksdorf, together affording the satisfactory separation of the plant from the species with which it has been hitherto confused, as well as from all other described species of the genus. It is fitting that this new *Camassia* bear Mr. Suksdorf's name, and the author takes great pleasure in dedicating it to him. A description is herewith appended:

Camassia Suksdorfii Greenman, n. sp.—Bulbs ovate, 1 to 2^{cm} in diameter: leaves narrowly lorate, 3^{dm} or less long, 0.5 to 2^{cm} broad: scape 3 to 7^{dm} high, few-flowered: bracts lance-attenuate, membranous, mostly shorter than the elongated 1–3.5^{cm} long arcuate-ascending pedicels: flowers regular, blue or in the dried state somewhat violet, fully 5^{cm} in diameter when completely expanded; perianth segments lanceolate, 3 to 3.5^{cm} long, about 8^{mm} broad, mostly 5-nerved, in the later stages closing over the ovary and becoming somewhat spirally twisted: cells of the ovary about 12-ovuled: capsule 1.5 to 3.5^{cm} long, 10 to 12^{mm} in diameter, obtusely angled: seeds ovate, 3 to 4^{mm} long.—Washington, in wet meadows, Falcon valley, *Suksdorf*, no. 251, June–July 1883, and July 1880, *Suksdorf*, no. 509; near Bingen, altitude 600^m, 21 May 1900, *Suksdorf*, no. 2663. A white-flowered form of this species was collected in a wet meadow in W. Klickitat county, Washington, altitude about 600^m, 19 May 1891, *Suksdorf*, no. 2023.

The species here proposed is distinguished from *Camassia esculenta*

Lindl. by the larger flowers, longer pedicels, which usually exceed the subtending bract, and by the larger fruit and seed. In the mature specimens the capsules are erect and disposed on arcuate-ascending pedicels, so that the fruiting raceme is 4 to 5^{cm} in diameter instead of 2 to 3^{cm} as in *C. esculenta*. From *C. Leichtlinii* Watson, to which Suksdorf's no. 509 was referred, *C. Suksdorfii* differs in the color of the flowers, the less sharply triangular, thinner, and less conspicuously nerved capsule. The seeds, moreover, in *C. Suksdorfii* are longer and have a more bluish luster than in *C. Leichtlinii*.—J. M. GREENMAN, *Gray Herbarium*.

CURRENT LITERATURE.

BOOK REVIEWS.

Vegetation der Erde.

THE VEGETATION of the Illyrian countries forms the topic of the fourth volume ² of this splendid series of monographs edited by Engler and Drude. The area covered by the work ignores political and to some extent phytogeographic boundaries, embracing the field which Dr. Beck has for many years made peculiarly his own. In a general way the region under discussion corresponds to the ancient Roman province of Illyria, and includes Servia, Montenegro, and the western portion of European Turkey, as well as the southern part of the Austro-Hungarian empire. The Slavic tongues dominate in most of the Illyrian regions, and many of the best botanical workers have been natives. Among those prominent in phytogeographic study have been Visiani, Sendtner, Vandas, Baldacci, Pancić and Adamović. Since 1886 Beck has published many important papers which have amply fitted him for this monograph. The bibliography includes about 800 titles.

After a brief treatment of the geography and climatology, the formations are described in detail. Among the most interesting of the formations are the well-known Mediterranean evergreen forests and thickets, in which forms with broad leathery leaves (Schimper's sclerophylls) dominate. The peculiar evergreen thicket, known as the maqui or macchie, is the most typical of Mediterranean formations and does not depart far from the sea; among the character plants are the arbutus, laurel, myrtle, olive, evergreen oaks, Spartium, juniper. This unique vegetation is believed to be due to the unique climate, the winter being mild while the summer is hot and dry. In some places near the sea *Pinus halepensis* is a leading plant, preceding the maqui rather than following it. Woods are also composed of *Pinus nigra*, laurel, and various oaks. Vast areas are covered by rocky heaths, especially in limestone regions; under favorable conditions near the sea a rock heath is an early stage of the maqui.

In the interior the forests are dominated for the most part by deciduous

² BECK VON MANNAGETTA, DR. GÜNTHER RITTER, Die Vegetationsverhältnisse der illyrischen Länder begreifend Südkroatien, die Quarnero-Inseln, Dalmatien, Bosnien und die Hercegovina, Montenegro, Nordalbanien, den Sandzak Novipazar und Serbien. 8vo, pp. xv + 534, with 6 full page plates, 18 text figures, and 2 maps. Leipzig: Wilhelm Engelmann, 1901. Subscriber's price M 20, bound M 21.50; separate price M 30, bound M 31.50.

oaks. *Pinus nigra* appears early in rock formations inland; with this exception there is little in common between the Mediterranean and inland forests. There are great areas of rocky heath inland having the physiognomy but not the floristic features of the heaths near the sea. The inland heath, too, is potentially a forest, while the coastal heath is an expression of the Adriatic climate.

A third section deals with the mountains and many interesting features are here described. There is a decided dominance of xerophytic associations, alpine meadows and similar formations being rare. Magnificent forests of beech, fir, and spruce characterize the lower portions of the mountains, just above the oaks. This forest type is not found on the seaward side of the mountains because of the severe climate, which permits only xerophytic trees like *Pinus nigra* to prosper. The beech approaches the lowlands more than do the spruce and fir, while the latter are more characteristic of the higher mountain districts. Various pines dominate in xerophytic areas. The sub-alpine thicket is composed of pine, juniper, and various other shrubs which form a typical "krummholz." The alpine plants embrace a large number of endemic species, but there are also many widespread forms.

The work concludes with some chapters on the floristic subdivision, history, and relationship of the Illyrian countries. Though the subdivision is purely floristic, rainfall is regarded as the chief distributional factor. The book is well up to the high standard previously set by Willkomm, Pax, and Radde. It is also of peculiar importance since it is the only available work which sums up for general use the broad facts of plant distribution in south-eastern Europe.—H. C. COWLES.

MINOR NOTICES.

KENNETH K. MACKENZIE, assisted by B. F. Bush and others, has published a *Manual of the flora of Jackson county, Missouri*.² It brings together the records of several local floras, beginning with the *Flora of Jackson county* by Mr. Bush in 1882. So far as the reviewer knows, this is the first manual with full descriptions and keys devoted to a single county published in the United States. The advantages of such a manual for local use are very evident, and the students of botany in Jackson county are specially favored. The book is exceptionally well printed, and with its keys, glossary, and indexes is a very complete manual. The summary shows that 1141 species and 51 varieties are included.—J. M. C.

A NEW disease of cultivated bananas near Alexandria, Egypt, has been noted for three years.³ It is characterized by a sudden check of growth, the leaf-points and central leaf blacken and die, putrefaction sets in and proceeds

²8vo, pp. xix + 242. Kansas City, Mo. 1902.

³FAWCETT, WILLIAM, A banana disease. Bull. Bot. Depart. Jamaica IX, 100-105.

downward in the latter, and the stem bears many small, crippled leaves. Nematodes were found to be the cause of the trouble. Recently the same disease has again appeared near Alexandria. Microscopic examinations showed that the nematodes were more abundant in the secondary roots than in the main ones. The secondary roots are destroyed, the food supply is thus cut off and the growth is checked in consequence. The matter is complicated by the presence of other species of nematodes. "Trap-crops" are suggested for the removal of most of the nematodes. This it is argued will remove so many that they will not be especially injurious. No other definite remedy is given.—P. SPAULDING.

NOTES FOR STUDENTS.

P. J. O'GARA,⁴ of the University of Nebraska, has conducted experiments which indicate that *Sphaeropsis rhoina* of the sumac and *S. malorum* of the apple are the same fungus. At least, the former will cause black rot in the fruit of the apple, and will also produce the typical "canker" on the branches just as readily as the latter.—J. M. C.

MRS. E. G. BRITTON and Miss A. Taylor⁵ have published an account of the morphology and anatomy of *Vittaria lineata*. The prothallium is irregularly branched and consists of a single plate of cells. It has remarkable powers of vegetative propagation and produces gemmae very similar to those described by Goebel for *V. elongata*. The antheridia are very numerous, and are produced either upon the ventral surface of the prothallium or upon the gemmae, and rarely upon the same prothallium as the archegonia. The development of the antheridium is of the usual polypod type, with funnelform wall and cap cell, and twelve or twenty-four sperms are produced. The long stalk of the sporangium seems to be formed chiefly by a single row of three or more elongated cells, longitudinal divisions occurring next to the spore-case. The interesting observation is made that the small stalk-cells at the base of the spore-case become very much inflated, and when the case opens they tilt it back. Long-stalked, branching, and multicellular paraphyses occur among the sporangia, the terminal cells being elongated, curved, and enlarged at apex.—J. M. C.

ITEMS OF TAXONOMIC INTEREST are as follows: SPENCER LEM. MOORE (Jour. Bot. 40: 305. *pl.* 441. 1902) has described a new African genus (*Amphoranthus*) of Caesalpineae from Damaraland.—E. L. GREENE (Pittonia 5: 1-56. 1902) has published 6 new species of *Acer*, 22 new species of *Microseris*, 14 new species of *Phacelia*, 7 new segregates of *Viola canadensis*, 8 new acaulescent violets, a revision of *Romanzoffia* (10 species, 8 of which are

⁴ Science 15: 434-435. 1902.

⁵ The life history of *Vittaria lineata*. Memoirs Torr. Bot. Club 8: 185-211. *pls.* 23-31. 1902.

new), a revision of *Capnorea* (14 species, 8 of which are new), 5 new species of *Cryptanthe*, and 3 new species of *Compositae* (*Helenium*, *Thelesperma*, *Vernonia*).—C. DECANDOLLE (Urban's *Symbolae Antillanae* 3²: 159-274. 1902) in his monograph of West Indian *Piperaceae* recognizes 70 species in *Piper* (21 new), 3 in *Verhuellia*, 79 in *Peperomia* (4 new), and excludes *Symbryon* Griseb.—JANET PERKINS (Engler's Bot. Jahrb. 31: 481-494. 1902) has completed her study of *Styracaceae* and has revised the genus *Lisianthus* (*Gentianaceae*).—ALICE EASTWOOD (Bull. Torr. Bot. Club 29: 523-525. 1902) has described new western species of *Castilleja*, *Lappula*, *Corydalis*, and *Campanula* (2).—H. D. DEBOISSIEU (Bull. Herb. Boiss. II. 2: 803. 1902) has described a new genus (*Melanosciadium*) of *Umbelliferae* from China, belonging to the *Smyrnieae*.—J. M. C.

PROFESSOR STRASBURGER, in his first paper⁶ on double fertilization, insisted that in fertilization two processes should be recognized: the stimulation to development and the mingling of ancestral qualities, the latter process being the essential one, and the stimulation to development only providing the conditions which make it possible to attain the advantages which result from a mingling of ancestral plasma masses. In a recent paper⁷ he defines very clearly his own views and makes critical references to recent work. Fluctuating variations do not furnish a starting point for the formation of new species. It is the principal function of fertilization, through the mingling of ancestral plasma masses, to keep the species characters constant. This view agrees with that of Richard Hertwig and approaches that of Solms-Laubach in so far as the latter regards "so-called fertilization," or the fusion of hereditary masses, as an essential element in fertilization; but Solms-Laubach regards the stimulation to development as an equally important attribute of fertilization. Strasburger, however, defines the "so-called fertilization" definitely as the union of the two hereditary plasma masses and believes that it was to insure this essentially "generative fertilization" that in the course of phylogenetic development the inability of the sexual cells to develop independently without fusion became more and more marked. The term "generative fertilization" is used to designate a union of ancestral plasmas, in contrast with "vegetative fertilization," which is merely a stimulus to development. Were it not for the fact that the two processes occur simultaneously, the distinction would have been recognized long ago. The term "fertilization" has often been loosely used in cases like many nuclear fusions in fungi, where there is no union of hereditary masses, but only a stimulus to development. While Strasburger would be willing to admit that the stimulus to development might be due to chemical or physical influences, he insists that "generative fertili-

⁶ STRASBURGER, ED., Einige Bemerkungen zur Frage nach der doppelten Befruchtung bei den Angiospermen. Bot. Zeit. 58: 293-316. 1900.

⁷ STRASBURGER, ED., Ueber Befruchtung. Bot. Zeit. 59: 1-8. 1901.

zation" is not a purely chemical process. Winkler suggests that bastards might be produced by chemical fertilization. Strasburger regards this as impossible and believes that the essence of fertilization lies in the union of organized elements. The view that the epigenesis of form is only an expression of the epigenesis of chemical power might, perhaps, appeal more to the physiologist than to the morphologist who has studied more deeply the developmental history of organisms. No doubt morphologists busied themselves too long with a one-sided mechanical view of ontogeny. If the chemical theory does not in the same way go beyond the mark, the two views united should be useful in extending our knowledge.—C. J. CHAMBERLAIN.

IN a rather extended paper Van Tieghem⁸ indicates his ideas of taxonomy as developed in the light particularly of researches upon ovular anatomy and morphology. For some time systematists have been familiar with the revolutionary attitude of the dean of French botanists, and his long successions of new families of plants have been duly noted in the bibliographies, but have not produced any general modification, either in Germany or America, of the current taxonomic sequences. Indeed, it would be a somewhat serious matter if it became necessary to rearrange herbaria upon the Van Tieghem system, since it is a complete *bouleversement* of the Engler-Prantl order, which has recently pretty generally superseded the old Benthamian arrangement of the families.

The object of M. Van Tieghem is apparently to develop a new classification founded upon the methods of reproduction in plants; how successful he has been must be left to the consensus of botanists to determine. The reviewer, after a careful examination, finds himself unable to follow Van Tieghem either in the general plan of his system or in the detail of its elaboration. To go over the points one by one would be impossible in a brief review, and I shall select but a couple of examples for criticism, believing that they will illustrate the system as a whole.

Van Tieghem begins by dividing the plant kingdom into two subkingdoms which he calls *Diodeés* or *Prothalleés* and *Adiodeés* or *Aprothalleés*. One finds that in the *Adiodeés*, which is the lower group, types from *Protooccus* to *Polytrichum* are included. Here too are such forms as *Vaucheria* and *Fucus*. In the *Diodeés* are the ferns and flowering plants. The distinction between the two subkingdoms according to Van Tieghem is the production of the eggs directly upon the "plant-body"—*naissance directement sur le corps adulte*—in the *Adiodeés*, and upon a special rudimentary body—the *prothallium*—in the *Diodeés*. Van Tieghem characterizes the former as "direct" formation of the egg and the latter as "indirect." Such a classification ignores the homologies established by Hofmeister and accepted

⁸VAN TIEGHEM, PH., L'oeuf des plantes, considéré comme base de leur classification. Ann. Sci. Nat. Bot. VIII. 14: 213-390. 1901.

universally since his time. It is at variance with modern ideas of alternation of generations and its significance. It fails to preserve the unity of the archegoniate series, but breaks it in two in the middle, separating closely related forms and throwing *Anthoceros* into one subkingdom and *Phylloglossum* into another. This is distinctly reactionary and opposed to the great current of embryological research from Von Mohl to Bower. The further subdivision by Van Tieghem of his *Diodeés* into *Exoprothalleés* and *Endoprothalleés* is equally artificial and objectionable.

Turning now to a matter of detail. Van Tieghem places at the bottom of his class *Homodiodeés* the *Inovuleés*, characterized by the absence of ovules. That brings the *Loranthaceae* practically to the bottom of the dicotyledons, a most improbable position for a group of metaspermic parasites. Reduction in such plants might be expected in connection with the high ecological specialization, but rudimentary structure would be altogether astonishing in the family to which the mistletoe belongs. It is rather in the aquatic medium that one would expect the primitive dicotyledons, and, indeed, in such plants as *Nelumbo*, investigated by Lyon, and *Ceratophyllum*, studied recently by Strasburger, the transition from the monocotyledonous to the dicotyledonous habit can be seen. No system that confuses reduced structures such as the placentation and ovule of the *Loranthaceae* with genuine rudimentary and simple structures can command wide adherence.

From top to bottom, both in the general and in the special portions, the Van Tieghem classification seems to be an inversion of the truth. Nevertheless, it is a distinctly ingenious and stimulating piece of work, and has already more than justified the labor spent upon it by its venerable and distinguished author, in the light it has thrown upon some of the smaller and more obscure groups of dicotyledonous plants. That it will be generally accepted is improbable, and it seems doubtful whether it will gain much currency even in France. The students of systematic botany, however, will be fully repaid by reading it, for it is both brilliant and interesting.—CONWAY MACMILLAN.

NEARLY FIFTY YEARS AGO there was described a species of *Dischidia* with remarkable double pitchers. Pearson⁹ now makes an examination of the phenomenon. He finds double pitchers in four species of the genus: *D. complex* Griffith, Malacca; *D. pectenoides* Pearson, n. sp., Philippines; *Dischidia* sp., Borneo; *Dischidia* sp., Borneo; the last two are undescribed, and in very imperfect condition. The pitchers in these species, as in the other pitcher-producing species of the genus, of which by no means all show this characteristic, are morphologically leaves, the inner surface of the pitcher being homologous with the under surface of the foliage leaf. The origin of

⁹ PEARSON, H. H. W. On some species of *Dischidia* with double pitchers. Jour. Linn. Soc. 35: 375-390. pl. 9. 1902.

the simple type of pitcher seems to result from an early arrest of apical growth and a rapid growth of the central portion of the morphologically upper surface with a consequent bulging out. In the double pitchers, the structure of which is described in detail, the inner pitcher may be supposed to have been formed first, since in the development of the pitchers of *D. Rafflesiana* apical and basal growth in the leaf ceases at an early stage, and the pitcher has assumed a definite form, so that in species with the double pitchers a resumption of apical growth, with the accompanying involution which gives rise to the inner pitcher, can hardly be supposed. As to the function of the pitchers, conclusions based on herbarium material must necessarily be unsatisfactory. Fairly complete investigations have quite conclusively shown that the pitchers of *D. Rafflesiana* are to be regarded as living "flowerpots," containing, as they usually do, water and soil and being supplied with a copious root system. In the four species under consideration, all of which are epiphytes, and clearly xerophytic in structure, the author was able to examine the contents of nine pitchers, all of which contained roots, and in all cases more or less soil in the outer but none in the inner pitchers. It seems, as Groom believes to be the case in *D. Rafflesiana*, that the greater the amount of soil the greater the development of roots in the outer pitcher. That ants bring the soil into the pitchers of these species the author of the paper considers certain, the ants making their nests in the pitchers. To what extent the plant depends upon the food material contained in these organs is unknown, but the indications are that they are of no inconsiderable importance. As to the benefit derived by the ants from this symbiotic relation, the pitchers are convenient shelters and nesting places, for which the four species may be assumed to be better adapted than *D. Rafflesiana*, on account of the narrower entrances and more commodious forms. As to the function of the inner pitcher, they may possibly serve as a place of refuge for the ants in case of danger from drowning. There is some indication, in *D. pectenoides* at least, of a possible function as a feeding ground, the food material being a sweetish substance, evidently a decomposition product. Examination of the inner wall of the outer pitcher reveals the presence of a dense web of superficial mycelium, the explanation of the presence of which was impossible. A similarity to forms described by Muller in the "fungus gardens" of some South American ants was noticed. *Dischidia*, then, shows a series of modified leaves more remarkable perhaps than any other known genus, the highest specialization of which is found in the four species here described, where the adaptation to the residence of ant colonies as well as the economy of water seems to have reached its highest point.—J. ARTHUR HARRIS.

EDGAR W. OLIVE¹⁰ has published a detailed account of the Acrasieae,

¹⁰ Monograph of the Acrasieae. Proc. Boston Soc. Nat. Hist. 30: 451-513. pls. 5-8. 1902.

whose problematical relationship to the Myxomycetes has been the subject of considerable discussion. The two groups of Acrasieae (Guttulinaceae and Dictyosteliaceae) agree in that the vegetative individuals assume the form of amoeboid cells which never pass through a swarm cell condition, and in that the individuals during the fructifying period unite to form colonies (pseudoplasmodia); but they differ widely in the general character and structure of their fructifications, the Guttulinaceae showing little or no differentiation, and the Dictyosteliaceae considerable differentiation both in structure and function. In certain forms two types of division were observed; one in the young individuals shortly after germination, occupying a number of hours and accompanied by prolonged nuclear changes that resemble karyokinetic division; the other during the subsequent active amoeboid condition, resembling direct division and taking place usually within a few minutes. In a discussion of the systematic relations of the Acrasieae, the author states that there can be no question as to the common origin of the Myxomycetes and the Acrasieae, but that when the two groups are carefully compared it appears unlikely that the former have been derived directly from the latter, since the amoeboid stage is in reality the only feature strictly comparable. The families and genera recognized are as follows: Sappiniaceae: *Sappinia* Dangeard (1 sp.); Guttulinaceae: *Guttulinopsis* Olive (3 spp.), *Guttulina* Cienkowski (4 spp.); Dictyosteliaceae: *Acrasis* Van Tieghem (1 sp.), *Dictyostelium* Brefeld (7 spp.), *Polysphondylium* Brefeld (3 spp.), *Coenonia* Van Tieghem (1 sp.). —J. M. C.

ONE OF DR. ENGLER'S latest conceptions, which is already beginning to find concrete realization, is a vast botanical garden, which shall display the characteristic plant formations of the world. The underlying idea in Dr. Engler's scheme is floristic rather than ecological, although typical edaphic plant societies find representation. He had already outlined in detail his plan for an alpine garden — this has received very favorable mention, and may be referred to somewhat fully in these pages at another time. In a pamphlet²² of nearly a hundred pages Dr. Engler gives a plan of the garden and states his ideas in full as to the floristic subdivision of North America north of Mexico. The four chief divisions are *Arctic*, *Subarctic*, *Atlantic*, and *Pacific*. The Arctic division is like that of Europe and is not treated. Subarctic North America is subdivided into eastern, central, and western districts (Bezirke). Atlantic North America is subdivided into four provinces; lake, Mississippi and Alleghany deciduous forest, south Atlantic evergreen, and prairie. Pacific

²² ENGLER, DR. ADOLF, Die pflanzengeographische Gliederung Nordamerikas erläutert an der nordamerikanischen Anlage des neuen Königlichen botanischen Gartens zu Dahlem-Steglitz bei Berlin. Separate reprint from Notizblatt Königl. Bot. Gart., Appendix IX. 8vo. pp. iv + 94, with plan and distribution map. Leipzig: Wilhelm Englemann. 1902. M 2.40.

North America is subdivided into three provinces: Pacific conifer, Rocky mountain, southwestern arid or semi-arid. All of these areas are further subdivided and characteristic formations and species are given in some detail. Occasionally there are errors to be found in the alignment of species, as might be expected in a paper which is largely a compilation from the works of Sargent, Brendel, Mohr, Kurtz, Pound and Clements, and others. However, the broad outlines of the work are remarkably true to the facts. It is particularly interesting to see Atlantic and Pacific America separated into primary divisions, recognizing that the great cleavage lines in the United States run north and south. Ecologists have always known that the plant formations of this country had such an orientation, but many students of floristics during the last decade have attempted to make their great cleavage lines run east and west. We may hardly regard the question as settled, but rather opened up for further study. The details in Engler's paper are remarkably true in most instances; indeed one is obliged to confess that it is the best floristic presentation of the vegetation of this country which has yet appeared. Though designed to indicate the plan of a botanical garden in Germany, it is nevertheless so important a contribution to American phytogeography as to be a necessary work of reference.—H. C. COWLES.

R. H. YAPP¹² has recently treated of the anatomy, biology, and systematic position of *Polyodium* (*Lecanopteris*) *carnosum* and *Polypodium sinuosum*. As to systematic position, he concludes that while that of *P. carnosum* has been a debatable one, both of the forms should be regarded as closely allied species, both from external features and internal structure. Both are Malayan epiphytes. *P. carnosum* grows only in the higher branches of trees and usually on fairly high mountains, where it forms thick encrusting masses often several feet in length; while *P. sinuosum*, whose creeping rhizomes not forming such thick masses as those of *P. carnosum* are frequently seen quite near the ground, and usually on the trunk itself or on the main branches of its host, is often found almost at sea level. The distribution of *P. sinuosum* is more extended than that of *P. carnosum*. The thick fleshy rhizomes of these epiphytes are tunneled by a system of galleries similar to those of *Myrmecodia* and *Hydnophytum*, and like them invariably inhabited by ants. The origin of the galleries is similar in the two species. About 1-2^{mm} from the growing point and after the differentiation of procambium and protoderm, the parenchymatous cells in certain definite areas undergo a more rapid increase in size than those of the remaining ground tissue, the difference in size becoming more marked farther back from the apex. These zones of tissue, whose cells have increased so remarkably in size with little or no division, are sur-

¹² Two Malayan myrmecophilous ferns, *Polypodium* (*Lecanopteris*) *carnosum* (Blume), and *Polypodium sinuosum* Wall. Ann. Botany 16: 185-231. pls. 10-12. 1902.

rounded by a zone several layers deep of relatively small brown cells, which has been developed by radial and longitudinal division during the increase in size of the cells of the included tissue. At a distance of 2^{cm} from the apex, the large cells, which have been filled chiefly with water, the walls having merely a film of protoplasm, break down, giving rise to the ant galleries, which are thus of lysigenous origin. The arrangement of the galleries is in both cases regular, although not exactly the same, a main ventral longitudinal gallery giving off two lateral series of galleries to the branches and two vertical series leading to the leaf-cushions, branching soon after leaving the ventral gallery to form two longitudinal series of dorsal chambers. Communication with the external air is secured by short passages excavated in the soft tissue of the younger parts of the stem by the ants themselves. While the function of the galleries is still somewhat obscure, the large-celled tissue seems to have been developed as a special water-reservoir, but its early disintegration may indicate an important function in the galleries, as aeration or to a slight extent absorption of water. There is no evidence that the galleries are an adaptation on behalf of the ants. In *P. carnosum* the marginal lobes upon which the sori are borne are reflexed at maturity so that they are turned upward, this being possibly an adaptation to secure the distribution of the spores during a strong wind, which would be most favorable for a high growing epiphyte.—J. ARTHUR HARRIS.

NEWS.

PROFESSORS HUGO DE VRIES and Julius Wiesner have been made members of the Accademia dei Lincei.

DR. N. L. BRITTON was in England during August and September completing his investigations of American Carices and Crassulaceae.

J. B. DANDENO, formerly instructor in botany at the St. Louis Normal School, has been appointed assistant in botany at the Michigan Agricultural College.

COULTER AND ROSE's *Monograph of the North American Umbelliferae* has been reprinted by the Department of Agriculture, and was issued September 22, 1902.

AMONG THE FALL ANNOUNCEMENTS of Henry Holt & Company is *Plant Physiology* by George J. Pierce; and among those of D. C. Heath & Company is *An introduction to Botany* by W. C. Stevens.

THERE WAS AN ATTENDANCE of forty-four in botany at Woods Hole this summer, including the staff and investigators. Among the latter were Professor Duggar, Drs. Miyake and Overton, and Mr. George D. Fuller.

L. COCKAYNE, whose fine work on the vegetation of Chatham island, New Zealand, will soon be reviewed in this journal, has been granted a passage in the government steamer to the Antarctic islands. He plans to sail during December and will carry on ecological and floristic studies.

THE BOTANICAL SOCIETY OF AMERICA will hold its ninth annual meeting at Washington, D. C., December 29, 1902, to January 3, 1903, under the presidency of Dr. B. T. Galloway. The address of the past president, J. C. Arthur, and a program of scientific papers will be given at the sessions.

A BIOGRAPHICAL SKETCH of the late Marc Micheli, prepared by C. de Candolle, and accompanied by a portrait and bibliography, is published in *Archiv. Sci. Phys. et Nat. Geneva* of July, 1902. The bibliography includes thirty-four botanical titles. Micheli was born October 5, 1844, and died June 29, 1902.

THE BUREAU OF FORESTRY has established a dendro-chemical laboratory in cooperation with the Bureau of Chemistry, to study the chemistry of forest products. The laboratory is in charge of William H. Krug, and its first work has been a study of the chemical composition of the wood and bark of various oaks (chestnut, white, red, and black) and the western hemlock.

DR. ALEX. P. ANDERSON has resigned his position of curator of the
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herbarium of Columbia University to become an expert to the syndicate now engaged in developing the new method of treating starchy grains, etc., recently discovered by Dr. Anderson in the laboratories of the New York Botanical Garden. Dr. Anderson is fitting up a laboratory for the continuance of his work at Minneapolis.—SCIENCE.

THE KIRBY LUMBER COMPANY, whose holdings are in southeastern Texas, has requested the Bureau of Forestry to prepare a working plan for its lands. The lumbering operations of this company extend over a tract of 1,250,000 acres of pine lands, which contain about 80 per cent. of all the long-leaf pine of Texas. This vast single body of virgin forest is uninterrupted except for the clearings around the villages and farms which it encloses.

THE EDITOR OF *Science* for the fifth year has published statistics in regard to the conferring of the degree of doctor of philosophy by American universities. It is of interest to botanists to know that during this period (1898-1902) fifty-three doctorates in botany have been conferred. The thirteen conferred during 1902 are as follows: W. A. Cannon (Columbia), G. P. Clinton (Harvard), J. W. T. Duval (Michigan), T. C. Frye (Chicago), C. S. Gager (Cornell), C. A. King (Harvard), A. A. Lawson (Chicago), B. E. Livingston (Chicago), Florence M. Lyon (Chicago), K. Miyake (Cornell), E. W. Olive (Harvard), R. H. Pond (Michigan), and C. E. Preston (Harvard).

DURING THE PAST SUMMER two ecological parties have been in the field from the University of Chicago. Dr. Henry C. Cowles, with a party of fourteen, has been studying the climatic and edaphic influences on the flora of Mt. Katahdin, Maine. The results were very satisfactory, since a large number of plants and photographs were collected to supplement the field observations. Mr. Henry N. Whitford, with a party of eight, has been working in the vicinity of Flathead lake, Montana. Mr. Whitford plans to stay through a part of October, and is making a detailed map of the region. Messrs. C. D. Howe and L. H. Harvey, and Dr. B. E. Livingston have been doing individual work in Vermont, Maine, and Michigan.

WE LEARN FROM *Nature* that at the Belfast meeting of the British Association in September, Professor J. Reynolds Green, president of Section K (Botany), delivered an address dealing with the position of research in plant physiology, and its importance in agriculture. Papers were presented as follows: The morphology and past history of the Araucarieae, by A. C. Seward and Sybille Ford; Internodes and their relation to morphological problems, by Percy Groom; The dorsiventrality of the Podostomaceae, by J. C. Willis; The function of the nucleolus, and The nucleus of the Cyanophyceae, by Harold Wager; Sex in the genus *Diospyros*, and Foliar periodicity in Ceylon trees, by H. Wright; Fossil *Nipa* seeds from Belgium, by Messrs. Seward and Arber.

BOTANICAL GAZETTE

NOVEMBER, 1902

ON THE DEVELOPMENT OF CERTAIN PIPERACEAE.

DUNCAN S. JOHNSON.

(WITH PLATES IX-X)

IN an earlier paper on *Peperomia* I stated (Johnson, 1900^a, p. 9) that *Piper* and *Heckeria* have "essentially typical Angiosperm embryo-sacs." This statement was based on observations covering the critical stages in the development of this structure. Since then I have studied the embryo-sac in these genera in detail, for the purpose of discovering any possible clue to the derivation of the peculiar type of embryo-sac found in the related genus *Peperomia*. The more important results of a study of these forms are given here, together with an account of the fate during germination of the various structures found in the fruit of *Peperomia*.

I. THE OVULE, SEED, AND FRUIT OF PIPER.

The two species of *Piper* studied were *Piper aduncum* L. and a species determined as *Piper medium* Jacq. The development of the former, as far as followed, agreed closely with that of *Piper medium*; it will therefore suffice to describe and figure the latter in detail.

The flowers of *Piper medium* occur rather loosely scattered on a spike 4 to 8^{cm} in length. In the development of the flower the three outer stamens appear first, then the three inner ones. Each stamen has four pollen-sacs (*fig. 1, ps*), and the whole development of the stamens shows no noteworthy peculiarities. Soon after the stamens are formed the wall of the ovary appears

as a usually three-lobed ring just within the inner row of stamens (*fig. 2, cp*). These lobes ultimately fuse together except the stigmatic tips (*fig. 1, st*), and form a rather fleshy ovary wall, with at first a broad, somewhat capitate tip (*figs. 5, 11*). Finally the ovary becomes somewhat barrel-shaped, and when ripe is about 2^{mm} long and 1.5^{mm} in diameter, while the withered stigmas appear as slight papillae at the upper end (*fig. 14, st*).

From an early stage of development there are found in the wall of the ovary numerous scattered oil-secreting cells with nucleated protoplasts (*figs. 5, 11, oc*). In the nearly ripe fruit the carpellary tissue is differentiated into three distinct layers, the outer including the epidermis. The latter is made up of slightly elongated cells with papillose outer walls. At the base of the ovary are found a few scattered, multicellular, pointed hairs similar to those found more abundantly on the base of the spike, and to those shown for *Heckeria* in *fig. 16*. The first layer of tissue below the epidermis is of several layers of rather loose parenchyma cells, among which are scattered oil-containing cells (*figs. 11, 14, 15, cp¹*). The second tissue layer is of from five to ten layers of closely packed cells, elongated longitudinally to the fruit and without interspersed oil-cells (*figs. 11, 14, 15, cp²*). While both these outer layers of the ovary wall are continuous around the whole circumference, the third and innermost layer is discontinuous and confined to the six longitudinal grooves in the integument (*figs. 14, 15, cp³*). This layer is made up of somewhat elongated cells with trabeculate walls, thickly interspersed with oil-cells. At the border between the second and third layers and opposite the grooves in the integument occur strands of vascular tissue (*figs. 11, 14, 15, vb*), showing from three to eight or ten tracheids in transverse section. These strands continue on into the loose parenchyma of the stylar region where the tracheids become considerably swollen and sometimes detached from each other (*figs. 11, 14*).

The ovule, which is terminal on the axis, arises just as the carpel lobes are closing in above. The two integuments appear nearly simultaneously just after the archesporial cell becomes distinguishable (*fig. 3, iin, oin*). The outer integument soon

becomes much longer than the inner and closes together above the latter (figs. 5, 6). The inner integument a little later becomes much thicker than the outer, of three layers except near the micropylar end, and finally forms the principal seed-coat (figs. 6, 11, 12, 13, 15, *inn*). One or two layers of cells of the outer integument are recognizable in the ripe seed. The inner walls of the inner layer are thickened with a granular deposit resembling that found in the inner layer of carpellary cells in *Peperomia*. The primary hypodermal archesporial cell divides before the integuments have developed far, to form a tapetal cell above and the definitive archesporial cell below (fig. 4, *tp*, *es*). The tapetal cell later divides further to form four or five layers of cells above the embryo sac in the ripe seed (figs. 8, 12, 13, *tp*), not however, forming so sharply marked a group of cells as in *Peperomia pellucida* (Johnson, 1900^a, p. 2). The single definitive archesporial cell becomes a megaspore directly, without further division. It increases greatly in size, as does its nucleus also (fig. 6, *es*), but in so doing does not encroach upon the cells above it in the nucellus in such a way as to indicate that these are anything other than tapetal cells (figs. 6, 7, 8, 9, *es*, *tp*). No evidence was discovered at any stage of the formation of sister megaspores destined to final absorption by the functional one, as in so many Angiosperms.

The division of the megaspore occurs soon after the inner integument has closed in to form a narrow micropyle above the nucellus. This division occurs in the manner so frequently described. Of the first two nuclei formed one goes to each pole and there each divides (fig. 7). The four nuclei thus formed are frequently found grouped rather closely in the middle of the embryo sac (fig. 8), or in other cases we find a pair near each pole. The eight nuclei formed at the next division soon group themselves in the typical manner to form the ripe embryo sac (fig. 9). The exact derivation of the polar nuclei has not been made out with absolute certainty, but there seems no reason to doubt from the condition shown in fig. 9 that it is as commonly found in the Angiosperms.

In the ripe embryo sac the large egg and the two smaller per-

sistent synergids have well-marked cell walls (*fig. 10*). The large endosperm nucleus is found in a considerable mass of protoplasm, usually near the middle of the embryo sac (*fig. 10, espn*). The distinct antipodals early become sunken in the very bottom of the embryo sac. They seem never to increase in number nor greatly in size, but persist, though slightly crushed, even in the ripe seed (*figs. 12, 13, 14*). During the ripening of the embryo sac it continues to broaden, and when the endosperm begins to form it is nearly globular (*fig. 13*), and in the ripe seed it may be even broader than long (*fig. 14*).

No clear evidence of fertilization or even of the penetration of the pollen tube to the embryo sac has been obtained. Many pollen grains were found on the stigma, some of which had evidently begun to germinate.

In the further development of the embryo sac the endosperm nucleus is at first most active. This nucleus divides repeatedly by mitosis. The daughter nuclei become distributed throughout the peripheral cytoplasmic layer of the embryo sac (*fig. 12*), and after twenty or more free nuclei have been formed cell-walls appear between and about these, and a peripheral layer of cellular endosperm is formed (*fig. 13*). Later the central vacuole is filled up with endosperm cells (*fig. 14*), probably by the division of those of the peripheral layer, since no free nuclei were discovered in the vacuole within the first layer of endosperm cells formed. In the ripe seed the endosperm forms a somewhat top-shaped mass of several hundreds of cells (*fig. 14*).

During this development of the endosperm the egg changes but little except in size at first (*figs. 10, 12, 13*), but later it divides up to form a globular embryo, which in the oldest seeds seen (probably ripe ones) consisted in longitudinal section of thirty or forty cells, and showed no differentiation save a slightly developed suspensor (*fig. 14*).

The synergids, like the antipodals, are long persistent (*figs. 12, 13*), though the former were not seen in the ripe seed.

In the mature seed the embryo is about 0.06^{mm} in diameter, the endosperm is 0.3^{mm} , and the whole seed from micropyle to basal wall 1.7^{mm} long by 1.2^{mm} broad in the middle.

The contents of the cells of the embryo in the seed seem to be chiefly protoplasmic. The cells of the endosperm possess large nuclei and are filled around this with a substance evidently chiefly proteid in nature, and probably similar in function to that to be mentioned in *Heckeria* and *Peperomia*. From the time the eight-nucleate embryo sac is formed the nucellus swells rapidly, and by the time the endosperm-nucleus begins to divide the cells of the nucellus are beginning to fill up with starch. In the ripe seed the cells of the nucellus are solidly packed with starch (*figs. 14, 15, psp*), except the cells near the micropyle and those of the peripheral layer of the nucellus generally, in which the starch grains are smaller and there is a somewhat larger proportion of protoplasmic contents. The crushed and distorted nuclei of the starch-filled perisperm cells are distinguishable even in the mature seed.

No seeds of this species capable of germination were available, but it is natural to suppose that the process of sprouting must resemble closely that to be described in *Heckeria* and *Peperomia*, in which genera the structure of the ripe seed is essentially that just described.

II. THE DEVELOPMENT AND GERMINATION OF THE SEED OF HECKERIA.

Material of both *H. umbellata* and *H. peltata* was available, but a complete study was made of the former only.

The ovary of this form arises as a ring-like outgrowth of the axis of the spike above a slightly peltate bract (*fig. 16*), and between the two stamens, which appear somewhat earlier than the carpels. The edges of this ring soon become three-lobed, probably indicating the presence of three carpels in the ovary; and as the walls of the ovary close in above, each lobe stretches out to form a somewhat elongated division of the stigma (*figs. 22, 24, st*). From the time the carpels close in above the ovule until the fruit is ripe, there are found scattered through the carpellary tissue oil-secreting cells, the protoplasts and nuclei of which remain active until a very late stage of development (*figs. 17, 22, 24, oc*). In the mature fruit these are still present and

completely filled with globules of an oily or waxy substance. The stigmas of the ripe fruit are much shrunken (*fig. 29*). The walls of the ovary near the base of the ripe fruit are of six or eight cells in thickness, the cells being generally elongated with the axis of the fruit but not clearly differentiated into layers as in *Piper medium*. The inner cell-wall of the inner layer becomes irregularly thickened with granular material, as in the case of *Peperomia pellucida*. About the upper end of the seed the tissue of the carpels becomes thickened to a mass of rather loosely packed, thin-walled parenchyma cells with oil-cells scattered among them. There are no definite vascular bundles above the very base of the fruit, but scattered tracheids occur, especially in the région just below the stigma. The outer cell-walls of the epidermal layer of the ovary are finely granulated. The hairs which occur abundantly on the bracts (*fig. 16*) are wanting on the ovary. The nucellus of the ovule arises in a strictly basal position, at about the time the walls of the ovary are closing together above. The single hypodermal archesporial cell is distinguishable somewhat later, and is undivided up to the time when the integuments appear (*fig. 17, arsp*). A tapetal cell and the definitive archesporial cell are formed in the ordinary manner (*fig. 18*), and before the integuments have closed above the nucellus the tapetal cell divides to two or three layers (*fig. 19, tp*), which persist in the ripe seed (*figs. 23, 27, 29*).

The two integuments arise in the usual way, and nearly simultaneously, from the base of the nucellus (*figs. 17, 18*). The outer integument develops far enough to close in above the inner (*figs. 19, 22*), and becomes two or three cells thick, but only the inner walls of the inner layer ever thicken greatly, and in the mature seed only the inner layer of cells of this integument is distinguishable, the outer layer being crushed against the surrounding carpellary tissue. The inner integument closes to a narrow micropyle, the cells of which finally grow over to interlock closely from opposite sides (*fig. 27*). This integument soon becomes three-layered, or it may become six-layered above, and in the ripe seed the walls of all these layers of cells become thickened and brown to form the principal seed coat.

The inner layer is made up of radially elongated, prismatic cells, the middle layer of periclinally expanded ones, and the outer of more or less cubical cells (*figs. 24, 25, 27*).

The mature seed is distinctly triangular in transverse section, but the surface of the fruit may be five or six-angled from the pressure of adjacent fruits upon each other in the closely packed spike.

The definitive archesporial cell gives rise immediately to a single megaspore, no indication of degenerating sister megaspores being seen (*figs. 19, 20, 21*). This single megaspore, after enlarging slightly, gives rise to two, four, and finally eight nuclei in the typical manner (*figs. 20, 21, 23*). The large egg and the two synergids, all with distinct cell-walls, occupy the upper end of the elongated embryo sac. The polar nuclei fuse to form a large endosperm-nucleus (*figs. 23, 25*), which may be located near either the base, middle, or upper end of the embryo sac. The antipodal nuclei collect at the extreme base of the sac and do not develop cell walls until somewhat later than the egg and synergids (*figs. 23, 25*).

At about the time of fusion of the polar nuclei the embryo sac ceases to elongate and begins to broaden rapidly, so that the mature embryo sac is nearly spherical in form (*fig. 25*). At this stage the egg and synergids are somewhat flattened against the upper end of the embryo sac, and the very large antipodals bulge into the cavity of the sac from below (*figs. 24, 25*).

As in the case of *Piper medium* mentioned above, the synergids and antipodals are long persistent (*figs. 26, 27*), though apparently not quite so long as in the latter genus. The number of antipodals found below the endosperm mass in the nearly ripe seed is frequently but three; sometimes, however, there may be as many as six or eight (*fig. 28*), which probably arise by the division of the three primary ones, after their cell walls are formed. The prominence of the antipodals here suggests that their function is an important one. They are placed at the base of the embryo sac, in what is probably the direct line of food transit to the sac, and perhaps play a part in the transmission or possibly in the elaboration also of this food material, though the

shape of the older embryo sac seems to indicate that their power of breaking down and absorbing surrounding tissues is not as great as in many other known cases.

The embryo sac becomes filled with cellular endosperm before the egg divides (*fig. 26*). The very first division of the endosperm nucleus has not been seen, but when four nuclei have been formed these are found to be separated by cell walls, so that I believe that a cell wall is formed immediately after the first and each succeeding division of the endosperm nucleus, and thus the endosperm is cellular from the very first. This feature of the development at once recalls the case of *Peperomia pellucida* (Johnson, 1900^a), but differs strikingly from that of the more closely related genus *Piper*, as described above. Similar marked differences in the mode of formation of the endosperm in closely related genera have been already noted by Hofmeister (1859, p. 555 *et seq.*), and Hegelmaier (1885, p. 92). Evidently peculiarities of this sort cannot be taken as adequate indications of relationship, as has been recently suggested by Cook (1902) in the case of *Nymphaea* and *Sagittaria*.

The cells of the endosperm of *Heckeria* are at first largely vacuolated and possess large nuclei. The first cell-walls formed radiate from the egg (*fig. 26*), but later the walls come in somewhat irregularly (*figs. 27, 28*). In the ripe seed there are two hundred or more endosperm cells surrounding the embryo, in from two to five layers, and occupying a broadly top-shaped space at the upper end of the seed (*fig. 29*). The vacuoles of the endosperm cells at this time are filled closely with proteid granules, except some of the cells near the embryo, which have but little contents.

The first division of the egg occurs some time after the formation of endosperm begins, whether in consequence of fertilization or not has not been made out with certainty. The direction of the first wall in the few cases seen is oblique, and the arrangement of the cells in the many older embryos seen make it certain that this is the general rule (*figs. 27, 28*.) In the ripe seed the embryo consists of several hundreds of small elongated cells, making a globular mass about 0.05^{mm} in diameter, undifferen-

tiated except for a slight projection above, which perhaps is a secondarily developed, rudimentary suspensor (*fig. 29*). As the embryo pushes down into the endosperm the latter seems to close in above so that the embryo often comes to lie nearly centrally in the endosperm.

The germination of the seed in *Heckeria umbellata* (*figs. 30, 31*) is essentially like that of *Peperomia pellucida*, and will be mentioned in connection with the discussion of this process in the latter genus.

III. THE GERMINATION OF THE SEEDS OF PEPEROMIA AND HECKERIA.

The ripe fruit of *Peperomia pellucida* is oval in form, with a slightly pointed upper end, being about 0.85^{mm} long and 0.6^{mm} wide. It is made up, beside the seed, of four or five layers of carpellary tissue. The outer or epidermal layer is made up of bulging, thin-walled cells interspersed with knob-like glandular hairs, perhaps hydathodes in function (*fig. 32*.) The inner layer of the ovary-wall is of very large cells, with coarsely reticulate outer walls and with the basal walls irregularly thickened with granular material (*figs. 32, 33*). Between this layer and the epidermis are two or three layers of delicate, flattened cells.

The seed proper is 0.6^{mm} long and 0.45^{mm} in transverse diameter. It is surrounded by a single integument, the two cell-layers of which have their walls thickened and of a very dark color. The inner walls of the outer layer of the integument fit against the cells of the perisperm, especially at the upper end of the seed, with a very wavy outline (*figs. 32, 33*). In an earlier paper (Johnson, 1900^a, *fig. 15*) I was misled, by the much more regular line of cell-walls separating the outer layer of perisperm cells from those within, into thinking this the line of separation between integument and perisperm. The interpretation given above is however the correct one, as has been shown by Campbell (1901, p. 3), and the lower index line from *int* in the *figure 15* referred to above should run only to the inner, wavy border of the inner of the two darkly shaded cell-layers. All of the cells represented as containing starch in this figure belong to the perisperm. The great bulk of the seed within the integuments is

made up of nucellar tissue, or perisperm, richly stored with starch (*fig. 32*), the grains of starch in the outer cells being finer and less abundant than in the inner ones.

Near the upper end of this perisperm mass, separated from the integument by but two or three layers of cells, lies the somewhat oblately spheroidal mass of endosperm (*fig. 32*). This mass is 0.09^{mm} to 0.1^{mm} in diameter, and is made up of forty or more cubical cells with darkly staining contents, including abundant aleurone grains (Johnson, 1900^a, *fig. 13*).

The embryo is rounded or slightly elongated, without a well-marked suspensor or other sign of differentiation, and lies at the upper border of the endosperm (*fig. 32*). It is surrounded laterally and below by one or two layers of endosperm. It is 0.035^{mm} to 0.04^{mm} long, and is made up of about fifteen cells.

In many sections of the ripe seed a group of cells, corresponding in position to a synergid, is found near the upper end of the embryo, and seems entirely distinct from the endosperm (Johnson, 1900^a, p. 6). Observations made thus far fail to show anything peculiar in the fate of this group of cells during germination. These cells and the six other peripheral cells outside the endosperm (Johnson, 1900^a, *fig. 13*) are soon crushed aside by the swelling of the latter in sprouting.

Seeds of *Peperomia pellucida* collected in Jamaica in August 1900 germinated readily in October of that year. They therefore do not need this long rest apparently necessary for the seeds of *Saururus cernuus* (Johnson, 1900^b, p. 369). The exact course of development, that is the time of ripening and the length of rest required by the seed under the normal conditions, must of course be followed out in the tropics. In Baltimore the behavior of the seeds is as described below, when allowed to germinate on wet filter paper or chopped Sphagnum, at a temperature of 15° to 20°, before an unshaded window, but not in direct sunlight.

No external change whatever is visible in the seed for about a week, except an immediate slight swelling of the carpellary tissue, but important changes are going on within. The embryo grows to 0.1^{mm} in diameter, remaining globular in shape, and is

at this time made up of two hundred and fifty cells or more (*fig. 33*). The endosperm cells divide actively, chiefly by anticlines, swelling meanwhile to encroach upon the perisperm, and upon reaching a diameter of 0.3^{mm} begin to burst the integument near the micropylar end, but remain as a complete sac about the embryo (*fig. 34*).

As germination continues the embryo elongates, the two cotyledons form below, and the primary vascular strand of the hypocotyl appears (*fig. 35*). The endosperm uses up the contents of the surrounding perisperm cells, crushing in their walls at first, and then pushes out above between the rent edges of the integument and carpel (*fig. 35*). In so doing it either pushes aside or carries up with it the persistent group of tapetal cells and the overlying stigmatic regions of the carpel. The embryo remains enclosed within the endosperm sac until it is 0.5^{mm} long or more, at which time the cotyledons are 0.15^{mm} or 0.2^{mm} long, and have each a rudimentary vascular bundle connecting with that of the hypocotyl.

Soon after this size is reached the rapid elongation of the embryo pushes at first the tip and then the whole of the radicle through the upper part of the sac of endosperm (*fig. 36*). Still later by the elongation of the cotyledons all but the tips of the latter are pushed out of the endosperm (*fig. 37*). A swelling of the radicle, somewhat below the middle, first indicates the limits of root and hypocotyl. Below this root hairs soon appear abundantly, and later secondary lateral roots (*figs. 37, 39*). Above on the hypocotyl and cotyledons, even while the latter are still enclosed by the endosperm, numerous glandular hairs and many stomata are formed (*figs. 37, 38*). Within the cotyledons between the vascular bundle and the upper surface of the leaf there is found at this stage a single layer of cells with darkly staining contents whose exact nature and function are as yet undetermined (*fig. 38*).

As the root of the seedling elongates it curves downward to enter and anchor itself in the substratum by numerous root hairs and secondary roots. Then the hypocotyl elongates and thus raises the cotyledons with the adhering endosperm in the air

(fig. 37). The endosperm at this time is closely in contact with the tips of the cotyledons and even forces its way in between them somewhat (figs. 35, 36). At the outer or upper part of the endosperm it is somewhat thickened and forms thus a collar which tightly grasps the tips of the cotyledons and fills completely the rent in the seed-coat (figs. 37, 38, esp). This collar evidently serves not only to hold the seed on the tips of the cotyledons, but also to prevent the exit and loss of any dissolved food material on its passage between the perisperm and the embryo. This collar must also prevent pretty effectually the entrance of water from without to dilute this food material, or of bacteria and fungi to destroy it. The walls of the endosperm cells are comparatively thin throughout, and no indication of thinner spots in their walls or those of the cells of the cotyledons was seen.

The endosperm cap, pushed on by the swelling cotyledons, finally crushes in the previously emptied perisperm cells, until it fills about half the bulk of the seed. After this the absorption may go on until practically all the starch is removed from the remaining perisperm cells, while the walls of these cells remain distended just as when full of food material (figs. 36, 38). When the seedling is about 15^{mm} high, the starch of the perisperm being then nearly exhausted, the wasted remains of the seed and fruit slip off from the tips of the cotyledons. Then the curve in the hypocotyl straightens out, and the cotyledons open out widely to allow the still very small plumule to develop and expand (fig. 39). During the transference of the starch from the perisperm to the embryo, cells of the former can be seen in which the end near the endosperm is nearly devoid of contents, except for a faintly staining, apparently slimy substance, while the opposite end is still closely packed with starch grains. The chemical changes taking place during this process and the exact mode of transmission have not been made out satisfactorily as yet, but it is hoped that these may be followed out in detail as soon as a supply of fresh seeds can be obtained.

The ripe seed of *Heckeria umbellata* differs from that of *Peperomia pellucida* somewhat in shape and size (figs. 29, 32), but

chiefly, for our present purpose, in the considerably more massive embryo of the former. This is however still undifferentiated except for the slightly developed suspensor (*fig. 29*). The process of germination is also practically identical in both species, except that the embryo becomes slightly more differentiated in *Heckeria* before bursting through the endosperm (*figs. 30, 31, 34, 37, 38*).

The point of chief interest in the germination of these genera, in addition to the deferring of the formation of the organs of the embryo to the time of germination, is the behavior of the scanty endosperm. The endosperm of *Peperomia* and *Heckeria* does not at any time during its development contain any considerable amount of starch, though a few scattered grains may appear in it during germination. These latter are perhaps portions of the carbohydrate which are temporarily fixed in solid form during transmission through the endosperm. The cells of this tissue in the ripe seed are pretty rich in protoplasmic contents, with large nuclei (Johnson, 1900^a, *fig. 13*), and the vacuoles are filled closely with aleurone grains. These facts suggest that the chief function of the endosperm in these genera is not the storage of ordinary reserve food material, as this function is served in these seeds by the perisperm. The later history of the endosperm here indicates, though absolute proof must come from careful chemical work, that it really serves as a digestive apparatus for breaking down and absorbing the material stored in the surrounding perisperm and passing it on to the embryo. If this interpretation is the correct one, then the endosperm here fulfills the function which in many other seeds is performed by a part of the embryo itself, as for example the scutellum of the grasses (Haberlandt, 1896, p. 212). The aleurone and denser protoplasmic contents of the endosperm cells gradually disappear as germination proceeds, but the cell-walls remain plump and uncrushed till a comparatively late period of development, except a few cells of the inner layer near the tips of the cotyledons (*figs. 36, 38*). The fact that the cell-contents disappear first from the inner layer of the endosperm might suggest that this material goes directly to the embryo, but it seems quite

as possible that it may pass to the outer layer and thus keep this in condition to continue the absorption of starch from the perisperm. Only a careful chemical study of the cell-contents of all these tissues during the progress of germination can decide these questions definitely.

The restriction of the functions of the endosperm to the passing on, during germination, of the food material without to the embryo within has, so far as I have been able to learn, been pointed out in *Saururus cernuus* only (Johnson, 1900^b, p. 370). Humphrey (1896, p. 16) suggested that the single, aleurone-containing layer of endosperm in *Canna* might have some such function, but did not follow this out in germination. In the germinating seeds of *Canna* I find that this layer of endosperm persists till a late stage of this process as a sac about the haustorium, the relation being such that material from the perisperm must pass through the endosperm to get to the embryo, and it seems probable that it may play the same part as that suggested in *Peperomia* and *Heckeria*.

In many other families it has been shown, by Hartz (1885) and others, that the storage tissue in the seed outside the embryo is perisperm, and not endosperm, as stated in the older (and many of the newer) books. This is true, for example, of the Polygonaceae, Chenopodiaceae, Phytolaccaceae, Caryophyllaceae, and others, and, contrary to the accepted authorities, there is present in a considerable number of these forms that I have studied a small amount of endosperm also. In all cases of these perisperm-containing seeds which were sprouted, the endosperm was found to persist for some time during germination, and thus to be capable of taking part in the transference of food material to the embryo.

Observations thus far made lead me to believe that in the perisperm-containing seeds mentioned the embryo sporophyte of the second generation is never nourished by the parent sporophyte directly, but always through the intermediate gametophyte. In general, then, we find that the food substance supplied to the embryo by the nucellus may pass through the endosperm and be stored in the embryo during the ripening of the seed, as in

Cucurbita and Phaseolus ; or secondly, the food may be stopped in transit between the nucellus and the embryo, and stored in the endosperm, there to be held during the resting period of the seed, and delivered over to the embryo only at the time of sprouting, as in Ricinus, Zea, and apparently all Gymnosperms ; or finally, the food supply for the developing embryo may be stored in the nucellus itself until the time of germination, when it is passed on to the embryo through the endosperm, as in Saururus, Peperomia, Phytolacca, Canna, and others.

IV. SUMMARY AND CONCLUSIONS.

Campbell has shown (1899, p. 453) that the nearly ripe embryo sac of *Peperomia pellucida* differs from that of all other Angiosperms studied up to that time in the presence of sixteen free nuclei derived from the megaspore nucleus. The writer found the same species to be peculiar also in the formation of the endosperm nucleus by the fusion of eight of these embryo sac nuclei, and in the persistence of seven others of these near the wall of the sac, one of them near the egg in the position of a synergid (Johnson, 1900^a, p. 4). The ripe seed has a single integument, contains an undifferentiated embryo of about fifteen cells surrounded by a very small endosperm, which is cellular from the two-nucleate stage on, contains chiefly aleurone, and is surrounded in turn by an abundant perisperm stored with starch.

The study of several other species of *Peperomia* by Campbell and the writer has shown that these agree with *P. pellucida* in the features noted.

The development of the ovary, ovule, and embryo sac in *Piper* and *Heckeria* differ widely in several respects from that found in the related genus *Peperomia*. The ovary in both genera seems to be syncarpous. Two integuments are found in both. A tapetal cell and a single megaspore are formed from the archesporial cell in each genus. The megaspore gives rise in the usual way to a seven-nucleate embryo sac. The antipodals and synergids are long-persistent. The embryo in the ripe seed is very small, of forty or more cells in cross section, and globular except for a very short suspensor.

The endosperm-nucleus of *Piper* divides to twenty or more free nuclei, and then simultaneously cell-walls are formed about all of these. In *Heckeria* the endosperm-nuclei are separated from the beginning by cell-walls. Both genera resemble *Peperomia* in that the endosperm is comparatively slight in amount in the ripe seed and contains no starch, an abundant supply of the latter being stored in the surrounding perisperm.

In the germination of *Peperomia* and *Heckeria* the swelling of the endosperm and embryo bursts the seed-coats, and the endosperm protrudes through the rent as a sac which continues to surround the embryo until after root and cotyledons are differentiated. The embryo is truly dicotyledonous. The root finally pushes out through the endosperm, but the latter remains about the tips of the cotyledons and imbedded in the seed till all the starch of the perisperm is absorbed.

The present studies have failed to show, in close relatives of *Peperomia*, any peculiarities in the development of the embryo sac which are clearly intermediate between that found in this genus and that of typical Angiosperms.

The striking differences in the mode of formation of the endosperm in these three related genera shows again, as has been demonstrated by Hofmeister (1859) and Hegelmaier (1885), that characters of this kind are often of no value as indications of relationship.

The position taken by the writer in an earlier paper (Johnson, 1900^a, p. 9), that these peculiarities in *Peperomia* are secondary, a view supported by Strasburger (1900, p. 293) and Goebel (1901, p. 806), seems still the most reasonable one.

The case of *Gunnera*, where Schnegg (1902) has shown that the embryo sac contains sixteen or more nuclei, and that the endosperm nucleus is formed by the fusion of eight or ten of these, might at first sight seem to indicate that we have here again the persistence of a character which Campbell believes to be primitive. A consideration of the evidently distant relationship of these genera, however, together with the fact that no other Angiosperm known shows any relic of this supposed primitive type, makes it probable that *Peperomia* and *Gunnera* have secondarily and independently developed this type.

As to the systematic position of *Peperomia*, the writer sees at present no reason to doubt that it is properly placed among the Piperaceae. Whether the Piperales as an order are to be regarded as very primitive forms is not so clear. It is, of course, possible that the absence of floral envelopes here is primitive. The presence of perisperm in the seed is a character found in many of the simpler orders of Angiosperms, but it has probably been secondarily acquired, since we find nothing in the higher Pteridophytes or Gymnosperms to suggest that it is primitive. A survey of the Dicotyledons shows that perisperm is at present known in the seeds of Piperales, Aristolochiales, Polygonales, Centrospermae, and Ranales. All of these orders, as has been pointed out by Schimper and Lesquereux, are old geologically, and possibly represent branches of a single stock or phylum of the Dicotyledons (see Bessey, 1897, p. 33). I am inclined to believe, as many of the older systematic writers have held, that the Piperales are much more closely related to the Polygonales than the position assigned them by Engler (1898) indicates.

Within the Piperales it is evident that the flowers of *Piper* and *Heckeria* are more complex in structure (probably primitively so) than those of *Peperomia*. This is indicated by the syncarpous ovary and the presence of two integuments. It is not clear to the writer that *Saururus* is "distinctly more specialized" than some of these higher Piperaceae, as suggested by Campbell (1901, p. 114), nor that the Saururaceae are derived from the Piperaceae.

The morphological features of the germination of the seed in *Peperomia* and *Heckeria* indicate that the aleurone-containing endosperm of these forms acts as a digesting and absorbing apparatus for transferring the starch stored in the perisperm to the embryo.

In several other genera, of the Cannaceae, Polygonaceae, Phytolaccaceae, Caryophyllaceae, and others, a thin layer of endosperm separates perisperm and embryo and seems to serve the function above mentioned. The embryo sporophyte is perhaps everywhere nourished through the gametophyte and not by the parent sporophyte directly.

I am under obligation to Captain J. Donnell Smith for the freest use of his library and herbarium material, and to Mr. W. C. Coker for collecting seeds of *Peperomia* and *Heckeria* in Jamaica.

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EXPLANATION OF PLATES IX-X.

Abbreviations used: *ant*, antipodal; *arsp*, primary archesporial cell; *br*, subtending bract; *cot*, cotyledon; *cp*, carpel; *cp^r*, external layer of carpellary

tissue (including epidermis); *cp*², middle layer of carpellary tissue; *cp*³, inner layer of the same; *em*, embryo; *es*, embryo sac; *esp*, endosperm; *espn*, endosperm nucleus; *hy*, hydathode; *iin*, inner integument; *in*, integument; *mp*, micropyle; *nc*, nucellus; *o*, ovum or egg; *oc*, oil-containing cell; *oin*, outer integument; *osp*, oospore; *plu*, plumule; *pn*, polar nucleus; *ps*, pollen sac; *psp*, perisperm; *rh*, roothair; *sg*, synergid; *st*, stigma; *sta*, stamen; *sto*, stoma; *tp*, tapetal cells; *vb*, vascular bundle tissue.

All figures are camera drawings, and all are from microtome sections except *figs. 1, 37, and 39.*

Figs. 1-15. Piper medium Jacq.

FIG. 1. Superior view of young flower; the stigmas are often three in number. $\times 30$.

FIG. 2. Tranverse section of an ovary slightly younger than that shown in *fig. 5*, showing indications of the three constituent carpels. $\times 50$.

FIG. 3. Longitudinal section of ovule at the beginning of formation of integuments. $\times 360$.

FIG. 4. Similar section after the formation of tapetum. $\times 360$.

FIG. 5. Longitudinal section of ovary when integuments have just closed in at the micropyle. $\times 50$.

FIG. 6. Longitudinal section of ovule from such an ovary. $\times 360$.

FIG. 7. Longitudinal section of a nucellus containing a four-nucleate embryo sac. $\times 360$.

FIG. 8. Similar section at a slightly later stage. $\times 360$.

FIG. 9. A similar section of an eight-nucleate embryo sac. $\times 360$.

FIG. 10. Longitudinal section of a ripe embryo sac; the nuclei of the synergids from the adjoining section shown in dotted lines. $\times 360$.

FIG. 11. Longitudinal section of a nearly full grown fruit. $\times 30$.

FIG. 12. Detail of micropylar region of same, with embryo sac showing multinucleate non-cellular endosperm. $\times 360$.

FIG. 13. Longitudinal section of somewhat older embryo sac, and adjoining portions of nucellus, showing peripheral layer of cellular endosperm; the synergids indicated in dotted lines are from the adjoining section. $\times 175$.

FIG. 14. Longitudinal section of ripe food and seed, showing relative development of embryo, endosperm, and perisperm. $\times 30$.

FIG. 15. Transverse section at about the middle of ripe fruit. $\times 30$.

Figs. 16-31. Heckeria umbellata L.

FIG. 16. Part of longitudinal section of spike, passing through three ovaries and their subtending bracts. $\times 360$.

FIG. 17. Longitudinal section of an older ovary and the enclosed ovule. $\times 175$.

FIG. 18. Longitudinal section of still older ovule showing tapetum. $\times 360$.

FIG. 19. Longitudinal section of still older ovule. $\times 360$.

FIG. 20. Longitudinal section of ovule with four-nucleate embryo sac. $\times 360$.

FIG. 21. Longitudinal section of slightly older ovule. $\times 360$.

FIG. 22. Longitudinal section of fruit with nearly ripe embryo sac. $\times 125$.

FIG. 23. Detail of embryo sac from section shown in last figure. $\times 360$.

FIG. 24. Longitudinal section of fruit with ripe embryo sac. $\times 50$.

FIG. 25. Embryo sac of same, with surrounding portions of nucellus and inner integument; synergids from adjoining section. $\times 360$.

FIG. 26. Longitudinal section of an older embryo sac with a several-celled endosperm. $\times 360$.

FIG. 27. Similar section of still older embryo sac with twelve-celled embryo. $\times 360$.

FIG. 28. Similar section showing six antipodals. $\times 360$.

FIG. 29. Longitudinal section of ripe fruit. $\times 55$.

FIG. 30. Longitudinal section of germinating seed; the perisperm above the dotted line has been exhausted of starch. $\times 75$.

FIG. 31. Similar section at a later stage of germination. $\times 30$.

Figs. 32-39. Peperomia pellucida Kunth.

FIG. 32. Longitudinal section of ripe fruit. $\times 55$.

FIG. 33. Terminal part of a similar section at an early stage of germination. $\times 175$.

FIG. 34. Longitudinal section of same at still later stage, showing tip of integument and carpel burst off by swelling of endosperm and embryo. $\times 30$.

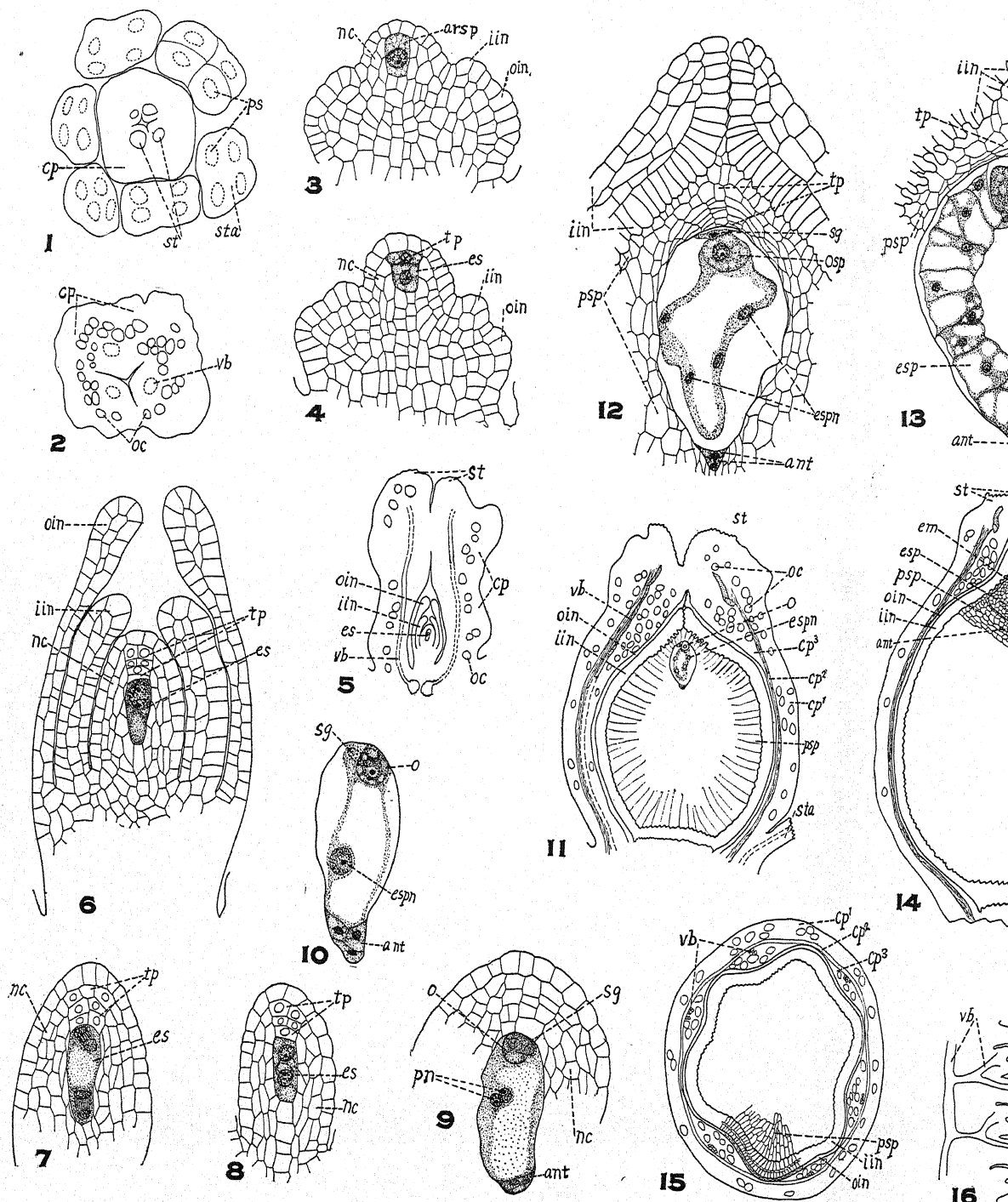
FIG. 35. Detail of embryo and endosperm of same. $\times 175$.

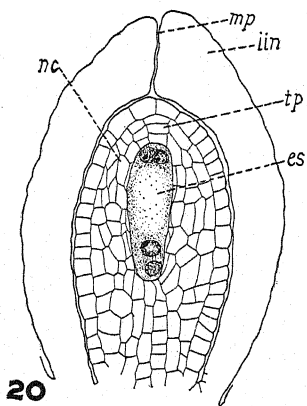
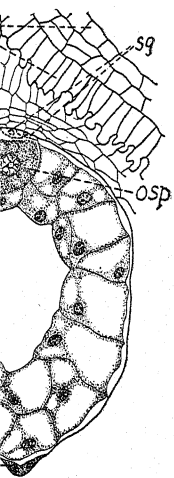
FIG. 36. Longitudinal section of germinating seed (with adhering carpelary tissue), showing radicle pushed out through endosperm. $\times 55$.

FIG. 37. Surface view of seedling with seed about ready to drop from the cotyledons. $\times 30$.

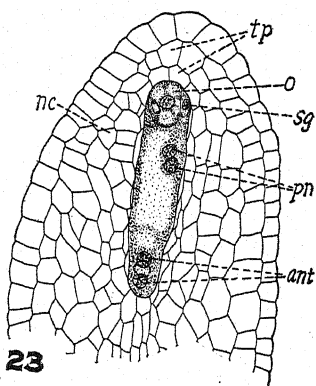
FIG. 38. Detail of same, showing seed and tips of cotyledons. $\times 50$.

FIG. 39. Seedling with expanded cotyledons, showing plumule. $\times 5$.

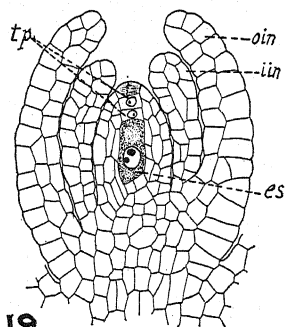
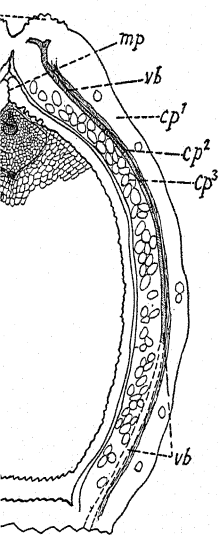




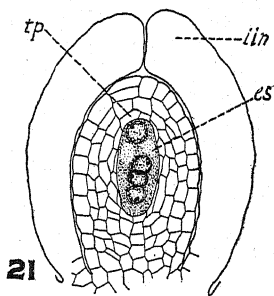
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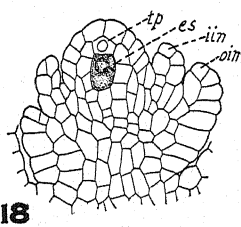
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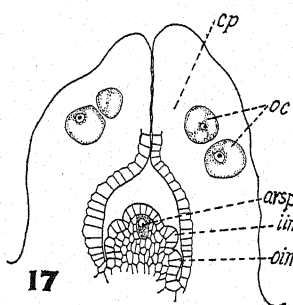
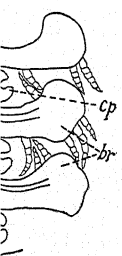
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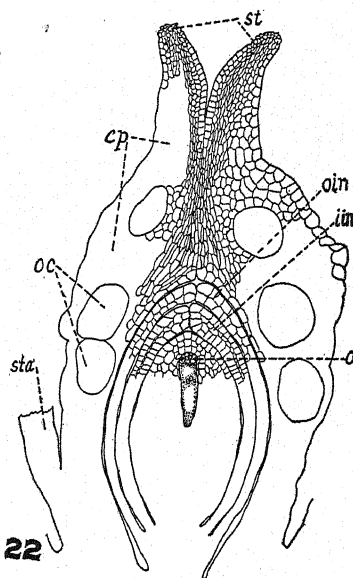
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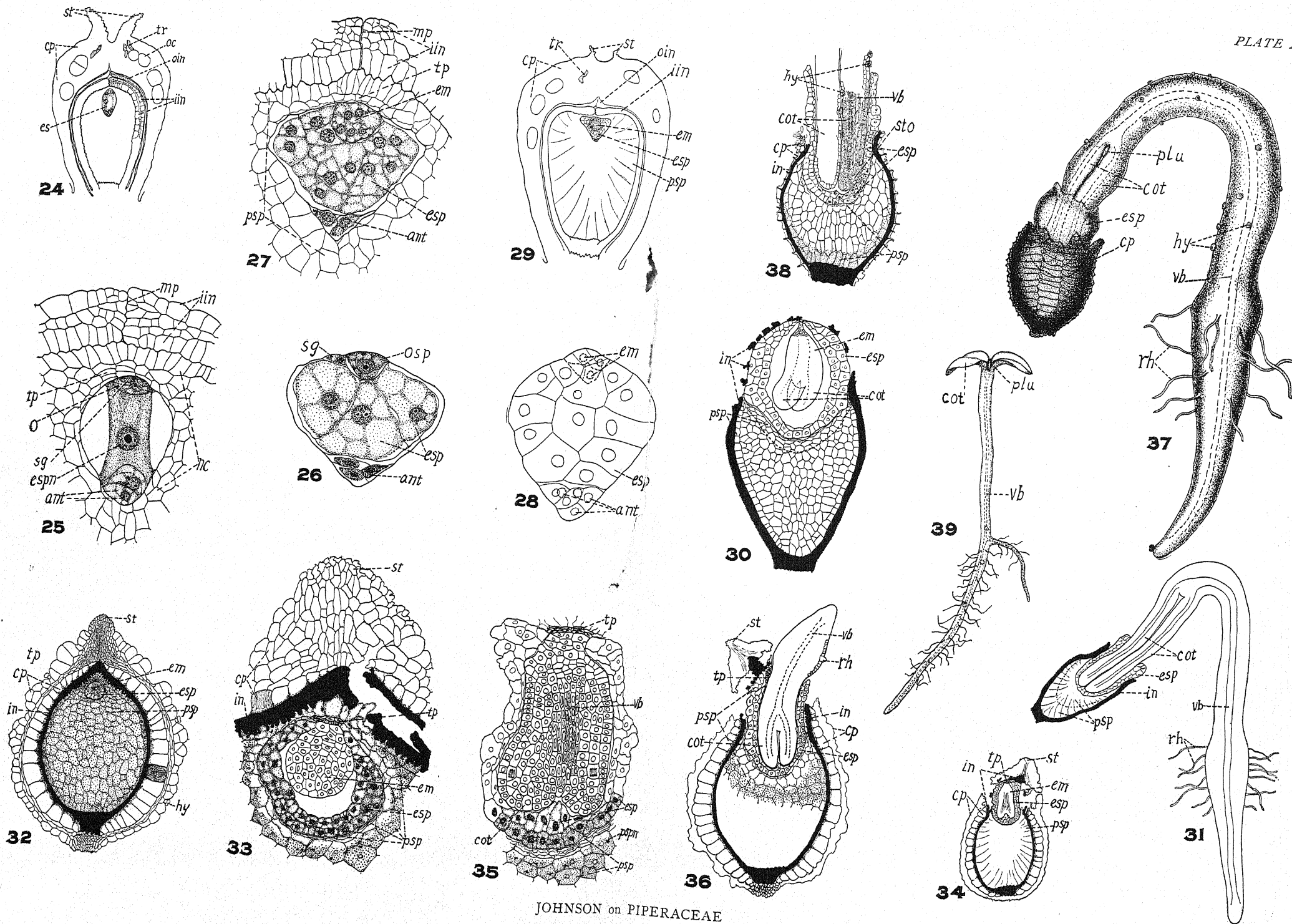
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22



JOHNSON on PIPERACEAE

THE STRUCTURE OF THE STARCH GRAIN.¹

HENRY KRAEMER.

(WITH PLATE XI AND TEXT FIGURES)

THERE have been a number of hypotheses advanced to explain the origin, nature, and structure of the starch grain. (1) It was originally considered to be a bubble filled with a liquid, or, as stated by Nägeli, "einer mit Flüssigkeit gefüllten Blase." According to Von Mohl, Raspail considered that the starch grain consists "aus einer in Wasser unlöslichen blasenformigen Hülle und einem löslichen gummiartigen Inhalte." (2) Then (1834) it was considered that to a central or excentral point layer after layer was added, the peripheral layers thus being the last formed, this view having been advanced by Fritsche (1) and supported in a more or less modified form by Treviranus (2), Lindley (3), Schleiden (4), Braun (5), Schacht (6), Crüger (7), and Unger (8). (3) Payen (9) in 1838 conceived the idea that growth took place from the outside, that through one or more funnel-like openings at the periphery of the grain new substances entered and new layers were formed therefrom, the outer layers thus being the oldest, in contradistinction to the view advanced by Fritsche. (4) Then followed a series of contributions in which the growth of the starch grain was likened to that of the cell wall and the formation of cells. This theory, with certain modifications, was advocated by Münter (10), Walpers (11), Reissek (12), C. Nägeli (13), Kützing (14), and Hartig (15). (5) While Nägeli (16) recognized that assimilation starch arose in plastids, he considered that most starch grains arose free in the cell sap under the influence of living protoplasm, and it was not until 1880 that Schimper (17) demonstrated that all starch grains develop within plastids and that in the reserve starch grains the leucoplastids finally disappear. Schimper further showed that the outer portion of the grain is the youngest,

¹An abstract of a preliminary paper on this subject was presented to the Society for Plant Morphology and Physiology, December 1899.

and thus substantiated the view of Fritsche concerning its development.

If we consult any of the standard works on organic chemistry, we find that the formula which is generally accepted for starch is $n(C_6H_{10}O_5)$, this being the formula recognized by Pfeffer, Tollens, and Mylius. It is supposed that the molecular composition is quite complex, the grain being composed of different single groups of $C_6H_{10}O_5$ or multiples of the same. While this formula may be accepted in a general way, still it has been shown that there are at least two substances which enter into the composition of the starch grain. Nägeli (16) has shown that the starch grain consists of two different substances, one which is soluble in ferments, and called by him granulose, and another which is insoluble in saliva, and called by him starch cellulose. He showed that when the starch grain was deprived of its water the lamellae were not apparent, and therefore he concluded that the layering was due to a difference in the amount of water present in the different lamellae. This view has given rise to the formula suggested by W. Nägeli (18) for the starch grain, which is $6C_6H_{10}O_5 + H_2O$, or $C_{36}H_{62}O_{31}$. Maschke (25) considered that the starch grain consisted of alternate layers of cellulose between which starch substance was deposited in two modifications, one soluble in water forming the light-colored lamellae, and another insoluble in water forming the dark layers. This view was not adopted, however, and Nägeli's theory prevailed until 1886, when Arthur Meyer (19) demonstrated that the substance termed cellulose by Nägeli, and which was termed "farinose" by Von Mohl (20), gave reactions similar to artificially prepared crystals of amyloextrin. In 1895 Meyer (21) further considered the composition of the starch grain and stated that it is made up of (1) α -amylose, (2) β -amylose, and (3) amyloextrin, a decomposition product of amylose. He also expressed the opinion that inasmuch as there is an anhydride of dextrose which does not readily take up water, there is probably also an anhydride of amylose which even on boiling with water is hydrated with difficulty, and that this is the substance that has given rise to the belief that there is

present a starch cellulose. This latter term, according to Meyer, has been used for a number of different substances: (1) mixtures of amyloextrin and α -amylose; (2) solutions of α -amylose and β -amylose; (3) solutions of β -amylose with various other substances, as nitrogen-holding substances, impure fatty products, pure amyloextrin, and the walls of plant cells which are contained in commercial starches unless carefully purified. He obtained the α -amylose upon treating starch paste (Stärkekleister) with malt solutions (Malzauszug) and by the action of hot dilute solutions of hydrochloric acid upon the whole starch grain. The portion remaining (β -amylose) is distinguished from the portion dissolved in that it is not soluble in water and becomes slightly reddish, and not blue with iodine.

One of the earliest views in regard to the development of the starch grain was that new layers were added to those previously formed, these being separated from each other by layers of air which were later called "Adhäsionsflächen," "Contactflächen," and "Grenzflächen" by Dippel (22), Strasburger (23), and Krabbe (24) respectively. These terms, however, have been mostly used by these authors in describing the structure of cell walls. In 1858 Nägeli (16) advanced the theory that the starch grain consists of elementary particles, later termed by him "micellae," which he supposed to have the form of parallelopipedal prisms with rectangular or rhomboid bases. Furthermore, according to Nägeli, these micellae possess a watery film, are embedded in a mother liquor which differs from them in composition, and are held together by certain forces. The growth of the starch grain is effected by the interpolation of new material among the particles already formed, this new substance being utilized in part in increasing the size of the micellae already formed, and also to form new micellae, which develop and arrange themselves according to the laws which the micellae previously formed have obeyed. This theory is known as the "intersusception theory," while the earlier one is spoken of as the "apposition theory." In addition to these two views in regard to the structure of the starch grain, Schimper (17) considered that it is made up of sphere-crystals which he called

"Spharokrystalloide." Meyer (21) has enlarged upon this view and considers the starch grain to be made up of two kinds of acicular crystals, which he calls "Trichiten," these being composed of α -amylose and β -amylose, there being also present in the grains that are colored red with iodine, amyloextrin and dextrin. He further says that most starch grains consist altogether or nearly so of amylose, and that these are colored blue with iodine. These latter starch grains are made up of sphere-crystals of amylose, arranged in layers, and these layers may consist of crystals of either α -amylose or β -amylose, or both, some starch grains containing in addition, as already stated, large amounts of amyloextrin and dextrin.

Starch grains are distinguished from one another by the following particulars: (1) The origin in the plant; (2) the shape of the grain; (3) the size of the grain; (4) the position of the point of origin of growth;² (5) the shape of the point of origin of growth; (6) distinctness of lamellae; (7) the direction of the lamellae; (8) behavior toward dilute iodine solutions; (9) the temperature at which the "Kleister" or paste is formed and its consistency; (10) the behavior toward various reagents, as chromic acid, calcium nitrate, chlor-zinc-iodide, sulphuric acid, diastase, etc.; (11) the appearance as viewed by polarized light. These differences in starch grains not only from different sources, but even in those of the same origin, tend to show that instead of starch being a uniform substance, it is made up of several substances, these occurring in varying proportions but appearing to be more or less definitely arranged.

The author may briefly state that he conceives the reserve starch grain to be the direct product of the polymerization of soluble carbohydrates of either the glucose or cane sugar group, together with the abstraction of water. This process is carried on under the influence of an organized body—either protoplasm, or a plastid, or both. The products thus formed consist of two

² The terms "hilum" and "nucleus" have been employed to distinguish the central or excentral marking, around which the lamellae or layers of the grain are arranged. These terms, however, are open to criticism, inasmuch as they are employed for another and specific purpose. The expression "point of origin of growth" seems to be better on account of its being less confusing, and is moreover descriptive and accurate.

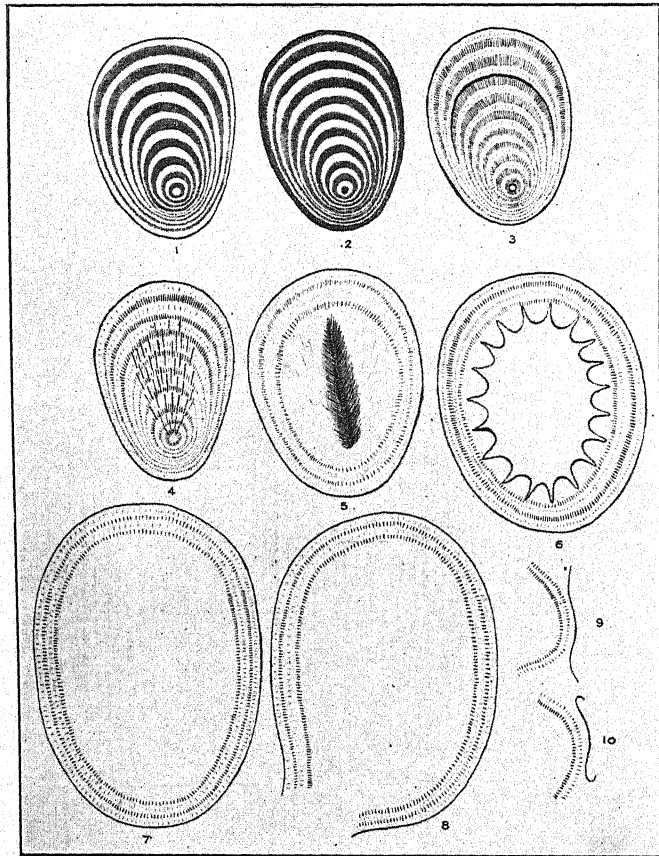
crystalloidal substances, namely starch cellulose³ and granulose, and also a colloidal substance. These occur as follows: (*a*) In the point of origin of growth we find the colloidal substance associated with a small proportion of cellulose as also in the alternate lamellae; (*b*) in the other layers occurs the granulose associated with a small amount of colloidal substance and possibly also some cellulose; (*c*) the peripheral layer of the grain is not readily acted upon by reagents and is quite elastic and more or less porous, probably consisting of an anhydride of cellulose; (*d*) in some cases some of the dextrins or some of the non-colloidal or crystalline carbohydrates, as maltose, dextrose, levulose, etc., may be present, but these are probably formed as a result of alterations taking place in the grain.

There have been a number of important contributions on the subject of the origin and structure of the starch grain, and while the views of the authors appear to be more or less at variance, still this is not to be wondered at, and it is highly probable that future observations will harmonize some of these conflicting views.

The illustrations of potato starch grains in the different textbooks show two kinds of grains, one in which the point of the origin of growth and alternate lamellae are light in color, as figured by Sachs (26); and the other in which the corresponding parts are dark in color, as figured by Strasburger (27). There is in reality no difference in these grains, this apparent difference being due to the manner of focusing upon them (*figs. 1, 2*), that is, whether viewing the lamellae from above or from below, or, as the Germans would say, by "tiefe oder höhe Einstellung." The two views of the successive lamellae thus obtained may be compared to the appearances obtained with two entirely different substances, the one corresponding to a more or less definite solid substance, as an oil globule, and the other to a body such as an air bubble (or vesicle filled with air or any other gaseous or

³Cellulose was a term first applied by Nägeli (16) and corresponds to the farninose of Von Mohl (20) and probably to the β -amylose of Arthur Meyer (21). Granulose another term which is generally accepted to have been coined by Nägeli (16), was adopted by Von Mohl (20) and apparently corresponds to the α -amylose of Arthur Meyer (21).

rarefied material). The appearance as observed in the oil globule corresponds to that of the layer next to the point of origin of growth and the layers alternating with it. The appearance of



FIGS. 1-10.—Potato starch grains, showing the effect of chromic acid and other reagents.

the air bubble corresponds to that of the point of origin of growth and the layers alternating with it. There is this difference, however, that instead of the purplish hue so characteristic of the air bubble, there is a reddish field in the starch grain which may be taken as indicating that it is of an entirely different

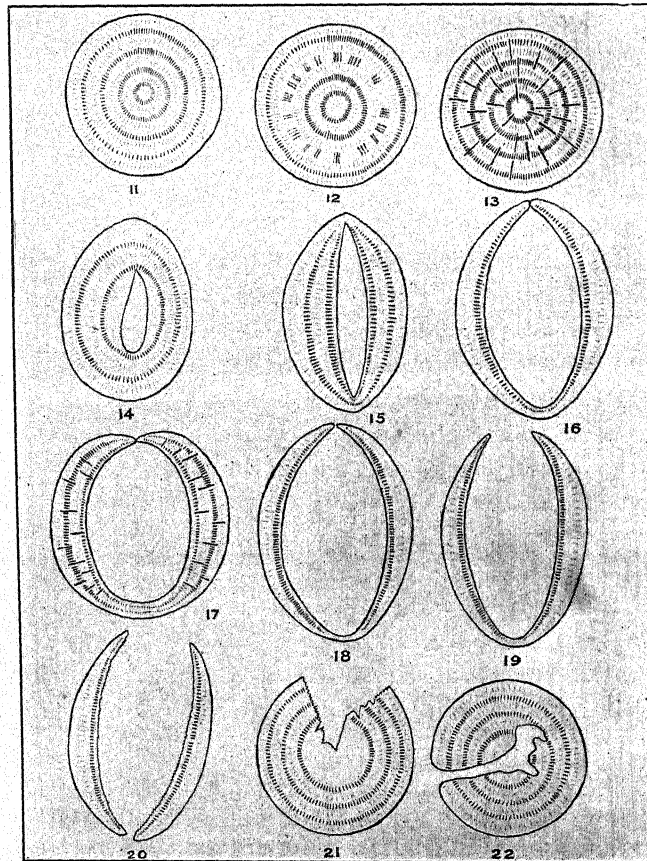
composition. A possible explanation of this phenomenon may be that in the air bubble the violet rays, owing to their length and velocity, completely overshadow the red rays; whereas in the starch grain the layers containing other substances offer a resistance to and refract the violet rays and leave the red only in view. As a result of this physical examination of the grain we observe that the successive layers differ in density, and that these correspond to the "water-poor" and "water-rich" lamellae described by Nägeli (16).

We further find in some of the potato starch grains that at the periphery of the point of origin of growth, as well as upon the inside of one or more of the layers corresponding to it, there is a dark line much resembling the peripheral layer of the grain (*fig. 3*). This probably led Dippel (22), Strasburger (23), and Krabbe (24), to consider that the lamellae did not differ in character, but that this appearance of lamellation was due to lines of contact, as already stated. Krabbe in the chapter dealing on the "Spiralstreifung der Bastfastern" further distinguishes between "Grenzflächen" and "Contactflächen." He says: "Schichten mit derselben Streifung, jedoch mit verschiedener Steilheit derselben, vorliegen, da wird ihre gegenseitige Abgrenzung dadurch noch deutlicher, das die Grenzflächen der Spiralbänder in der Contactfläche der Schichten nicht immer aufeinander Stossen."

A further evidence that there is a marked difference in the layers of the grain is the effect produced by staining reagents (*figs. 29, 30*). On treating starch grains with weak aqueous solutions of safranin and gentian-violet,⁴ it is observed that certain parts of the grain take up these stains more readily than others. The gentian violet stain is more pronounced in its effect upon the potato starch grain (*fig. 35*), it being held by the point of origin of growth and the lamellae alternating with it. Safranin, on the other hand, is a better differential stain for wheat starch grains (*figs. 36, 39*), being held in certain of the lamellae (usually not more than three or four of them being affected) and in numer-

⁴The method used by the author consisted simply in treating the freshly isolated starch grains, or the commercial starches, with weak aniline dye solutions and allowing them to dry at an ordinary room temperature.

ous radial clefts or channels. Corn starch (*fig. 40*) does not appear to take up these stains as readily as either wheat starch or potato starch, and there is no differentiation of the lamellae.



FIGS. 11-22.—Wheat starch grains; 11-20, showing the effect of chromic acid and other swelling reagents; 21-22, showing a direct disintegration of the grains through the action of ferments.

This is probably due to the peripheral layers being denser and less permeable. Salter (28) in speaking of the staining of the grain says that it is dependent upon the absorption of the aniline dye, and that in no case does it seem to have a selective or

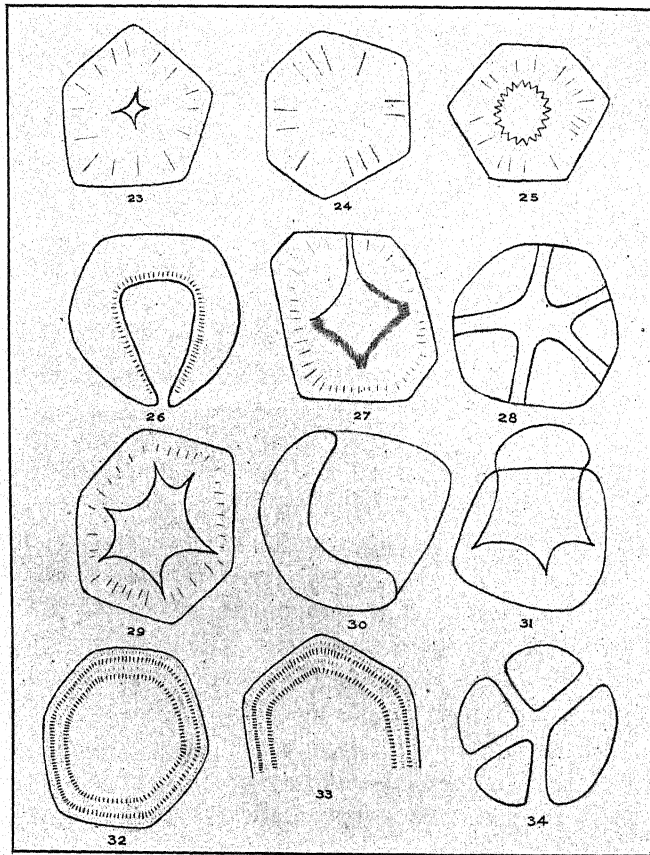
specific action on the layers. The figures of Salter, however, show that the stain is taken up by certain parts of the grain more than others, and in another place he states that "die Lamellen die im frischen Stärkekorn als dunklere Linien erscheinen sind diejenigen welche den Farbstoff am reichlisten einsaugen." In speaking of Meyer's work he goes on to say: "Meyer erwähnt dass bei der Färbung mit Methylviolet der Farbstoff besonders von den weicheren Lamellen beibehalten wird." The only unfortunate thing is that we do not know to what layers these authors refer when they speak of "weicheren Lamellen" and lamellae with "dunklere Linien." There seems to be no doubt, however, that what they have in mind corresponds to my own observations, that is, it is the layers which are colloidal in character which take up the stains; in other words, the point of origin of growth and the layers alternating with it.

Another interesting feature serving to differentiate the layers of the starch grain is the behavior toward dilute iodine solutions. The layers which are not affected by the aniline stains become blue with iodine, the alternate layers and the point of origin of growth remaining unaffected. The layers thus affected by iodine are the ones which are rich in granulose and are more clearly defined in the grains of potato and wheat starch than in corn starch. These layers become crystalloidal in character on treatment with water at 60° or 65° C. for about an hour, and also with chromic acid, calcium nitrate, saliva, and other reagents.⁵

The behavior of potato starch toward these reagents may be briefly summarized as follows (*figs. 1-10*): The first effect of the reagent is to make the lamellae more distinct (*figs. 1-2*); this is followed by the development of the crystalloidal character of the lamellae (*fig. 3*), which is most pronounced in those colored blue with iodine; this is followed by the production of small tracts or channels (*fig. 4*) connecting the contiguous lamellae, particularly in the middle of the grain; succeeding this there is the formation of channels which are larger and plume-like in appearance (*fig. 5*), the grain meanwhile swelling quite percep-

⁵Proc. Acad. Nat. Sci. Philadelphia 53: 450. 1901.

tibly, the middle portion becoming clearer and assuming a zigzag outline (*fig. 6*), between which and the periphery of the grain a number of crystalloidal lamellae arise (*fig. 7*); the



FIGS. 23-34.—Corn starch grains, showing the effect of chromic acid and other swelling reagents.

grain now becomes spherical and marked by a number of concentric lamellae near the periphery; the latter finally ruptures (*fig. 8*) and then follows a gradual solution of the grain, the peripheral layer sometimes recurving like the cutin layer of an epidermal cell on treatment with sulphuric acid (*figs. 9, 10*).

In wheat starch (*figs. 11-22*) the development of the crystalloidal character of the lamellae (*figs. 11, 12*) is followed by the formation of narrow, interrupted or continuous, radial channels near the periphery of the grain (*fig. 13*), which are sometimes connected with lamellae occurring near the middle of the grain; the grain meanwhile swells quite perceptibly, the center becomes clearer (*fig. 14*), the contents are crowded into crescent-shaped halves which are still slightly connected at the poles (*figs. 15-17*); the contents of each of the halves of the grain consist of crystalloidal lamellae in which are then produced small tracts or channels connecting the contiguous lamellae (*fig. 17*); the halves in some instances finally separating and slowly dissolving (*figs. 18-20*). In some cases, on the other hand, there is a corrosion of the grain at the periphery, followed by gradual disintegration without the separation into halves (*figs. 21, 22*).

The first effect of reagents upon the corn starch grain (*figs. 23-34*) is to bring out the point of origin of growth (*fig. 23*), the latter becomes larger and in some cases more or less zigzag (*fig. 25*) in outline; between this and the periphery of the grain arise more or less interrupted or continuous radial channels (usually the latter); the crystalloidal structure of this grain develops slowly and is most pronounced when the grain has swollen to two or three times its normal size; at this stage we find that the center of the grain has become clear and the point of origin of growth has become obliterated in some cases (*fig. 24*), and between it and the periphery occur numerous crystalloidal lamellae similar to those observed in the potato starch; finally the peripheral layer ruptures and there is a gradual disintegration of the grain (*figs. 26, 30, 33*). Sometimes the grain appears to separate into as many parts as there were arms to the point of origin of growth (*figs. 27, 28, 34*), particularly when acted upon by saliva or diastase.

A number of authors since the time of Nägeli have shown that the lamellae of starch grains differ in constitution and structure, and that there are at least two distinct kinds of lamellae. This view is confirmed not only by a microphysical examination of the grain, and by treatment with weak solutions

of iodine and aniline stains, but also by treatment with water and various reagents as just pointed out. Both Salter and Meyer appear to hold to the theory that there is a distribution of crystalloidal substance in particular lamellae. Salter quotes Meyer as saying: "die schattierten Schichten bedeuten die schwach lichtbrechenden relativ lockeren, an fester Substanz relativ armen, an Interstitien reichen Schichten, die hellen sind also die stark lichtbrechenden Schichten aufzufassen, welche die meiste feste Substanz enthalten." Here again it is unfortunate that the descriptions do not enable us to determine which layers are meant. It is likely, however, that the layers described as "schattierten Schichten" are the colloidal layers, and those designated as "hellen Schichten" are the crystalloidal layers.

In summing up the observations herewith presented, we find that the starch grain consists of colloidal and crystalloidal substances, these being arranged for the most part in distinct and separate lamellae, that is, at the point of origin of growth, and in the alternate lamellae the colloidal substance preponderates, associated with the crystalloid cellulose; whereas in the other layers the crystalloidal substance, consisting for the most part of granulose, occurs in greater proportion.

As a further evidence of the presence of these crystalloidal and colloidal areas we may say that the peculiar behavior of the colloidal layers toward aniline stains is analogous to the behavior of a section containing mucilage cells toward these dyes, the latter being taken up by the mucilage cells alone. Furthermore, as the characteristics of mucilage cells are most pronounced in anhydrous media, as concentrated glycerin, so a similar effect is observed in the starch grain, but owing to the action of the glycerin in readily forming soluble starch, the preparations of the starch grain, like that of the cell wall, when thus stained are best preserved in Canada balsam.

The crystalloidal character of certain of the lamellae as observed in connection with the swelling of the grain might be considered to be in the nature of microscopic clefts, but it should be said that we know of no colloid that behaves in this manner, and such an assumption does not seem to be well

founded. Furthermore, this appearance (crystalloidal) might be considered as due to an internal folding of the substance of the lamellae, but this would only arise in case of a contraction or reduction in the area of the lamellae; but as we have already seen the grain is swollen from two to four times its original size, and even in the fragments of the disintegrating grains the crystalloidal character is pronounced. It seems more likely, as I have already pointed out, that the reason this structure is not apparent under natural conditions is because the refractive properties of the crystalloidal substance so nearly resembles that of the associated colloid. The use of certain reagents, however, which are more or less penetrating in their action, cause an imbibition of water by the colloidal portions with consequent swelling of the grain, and hence a contrast in refractive power with the more insoluble crystalloidal substances.

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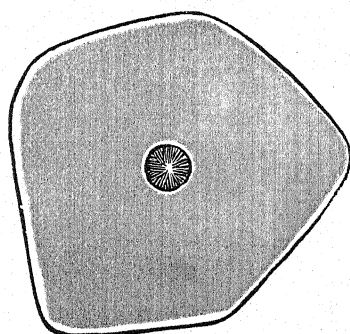
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EXPLANATION OF PLATE XI.

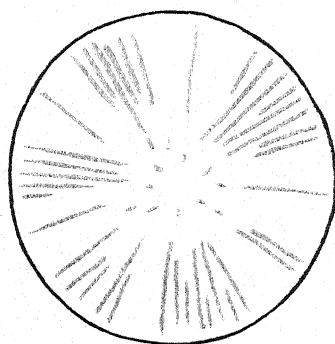
FIG. 35. Potato starch grain treated with weak aqueous solution of gentian-violet.

FIGS. 36-39. Wheat starch grains treated with weak aqueous solution of safranin.

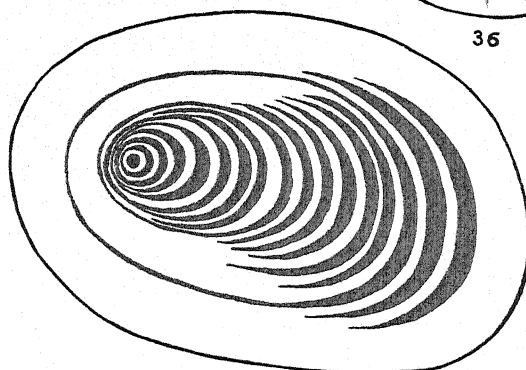
FIG. 40. Corn starch grain treated with weak aqueous solution of safranin.



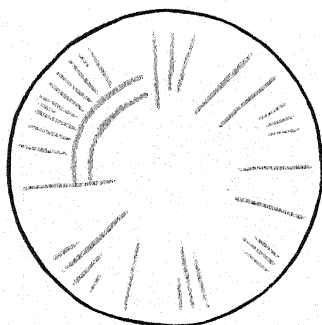
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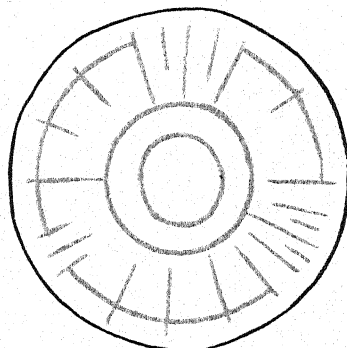
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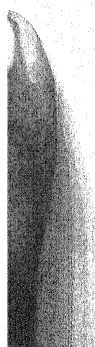
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38



39



CONTRIBUTIONS FROM THE ROCKY MOUNTAIN HERBARIUM. IV.

A VEN NELSON.

SOME CHENOPODIACEAE.

PROBABLY the most characteristic plants of the great saline plains of the West and the similar basins of the intermountain country are the Chenopodiaceae. Some of the genera in this family are known by name, at least, to most people. Such, for example, are greasewood, the salt-bushes, winter-fat, Russian-thistle, etc. Many of the species in this family are of remarkably wide distribution. As they become better known it is found that the range of some, once supposed to be quite circumscribed, is really quite extended. The strongly alkali-impregnated areas are so inhospitable that most plants are unable to occupy them, and nearly all the members of this family have in some way become tolerant of such soils. So far as the effect upon vegetation is concerned, all of the saline districts are essentially the same, the differences in the soil being apparently one of degree rather than of quality. This fact coupled with another, that this family has little competition on this kind of soil, may account in a measure for the unusually wide range of some of the species. Of course the other factors of environment are operative upon these plants as upon others, but they seem less potent than the soil in producing specific variation.

ATRIPLEX.

The foregoing remarks have been suggested by a rather extended study of certain species of *Atriplex* occurring within the Rocky mountain region. Not satisfied with the view afforded by the specimens in the Rocky Mountain Herbarium, the loan of another large collection was solicited.¹ Some notes

¹I wish to express my thanks to Dr. William Trelease, Director of the Missouri Botanical Garden, for the privilege of examining all the specimens illustrating the species considered in this paper which are contained in the Engelmann herbarium and the general herbarium of the Garden.

upon the results of the examination of this material may be of interest, especially since it served, in part, to disclose the new species herein proposed.

ATRIPLEX CANESCENS (Pursh) James, Catalogue 178.—This well known species is strongly marked by its winged fruits, and is more widely distributed than any of the species known to the writer. A very large series of specimens, covering a range extending from the Dakotas to California, show no marked differences, none sufficiently constant to constitute even a geographical form.

Atriplex aptera, n. sp.—Perennial, from a woody base, the annual stems fascicled, decumbent at base or even depressed, more or less branched, 1–3^{dm} high: leaves narrowly oblong, 2–4^{cm} long, 5–8^{mm} broad, mostly obtuse, the base cuneately narrowed to a sessile base: fruiting spikes paniculate, crowded, bracteate; the bracts linear-lanceolate, gradually reduced upward or wanting: dioecious, only the pistillate plant seen; fruiting bracts united, scarcely stipitate, somewhat indurated, densely scurfy, appendaged with three or four more or less vertical rows of short vertically flattened processes, some of these often expanded but scarcely wing-like.

This is the only species that makes a close approach to *A. canescens*. It is readily distinguished, however, by its smaller size, less woody condition, and the wingless scurfy fruits. *A. canescens* occupies dry clay, chalk, and marl cliffs and ridges; while *A. aptera* occurs (so far as known) on moist saline flats. It is a most excellent forage plant. The type is *Elias Nelson* 738, Laramie, Wyoming, September 1901.

ATRIPLEX HYMENELYTRA (Torr.) Wats. Proc. Am. Acad. 9: 119.—The remarkable fruiting bracts will not permit this species to be confused with any other. From the available specimens it would seem that it does not come into the Rocky mountain region proper, but extends from southern Utah into southern California.

ATRIPLEX CONFERTIFOLIA (Torr.) Wats. Proc. Am. Acad. 9: 119.—This is peculiarly a Rocky mountain plant, but has an extended north and south range, in fact across the United States.

ATRIPLEX ACANTHOCARPA (Torr.) Wats. Proc. Am. Acad.

9: 117.—Though sometimes attributed to Colorado and Utah, it is doubtful if it comes so far north. The Colorado and Utah plants usually so named may stand as follows:

Atriplex cuneata, n. sp. — Perennial, with woody base, from two to several decimeters high, branched from the base, the branches decumbent: leaves numerous, on the erect branches of the current year, 1–3^{cm} long, entire, thick or semi-fleshy, from narrowly to broadly elliptic, obtuse at apex, cuneately tapering into a short petiole: flowers dioecious; the staminate densely clustered in the upper leaf axils and in terminal spikes; the pistillate axillary, one or more in each cluster: fruiting bracts united except at the tip, thickened and forming an ovate or subglobose fruit, rather thickly covered with irregular, rigid, flattened processes.

This species is closely allied to *A. acanthocarpa* (Torr.) Wats., in fact is probably included, in part, in Watson's description (Proc. Am. Acad. 9: 117). It is probably not a part of *Obione acanthocarpa* Torr. Bot. Mex. Bound. 183. In any case, we must consider the typical form of that species as erect; the leaves thin, undulate margined, oblong or lanceolate, usually acute and many of them subhastate. Excellent specimens of typical *A. acanthocarpa* and of the now proposed species show marked differences in many respects, which will account for the fact that the latter has as often been distributed as *A. Nuttallii* as under the former name. Its range seems to be from western Colorado into Utah and south to New Mexico and Arizona.

SPECIMENS EXAMINED: *Chas. Wright* 573, expedition of 1849; *Brandegee* 1086, S. W. Colorado, 1875, in the Hayden Survey; *Alice Eastwood*, Grand Junction, Colorado, 1891; *M. E. Jones* 5443, Emery, Utah, 1894 (type, in Rocky Mt. Herb.); *Baker, Earle*, and *Tracy* 420, Mancos, Colorado, 1898; *Myrtle Zuck*, Holbrook, Arizona, 1896.

ATRIPLEX NUTTALLII Wats. Proc. Am. Acad. 9: 116.—This is preeminently the characteristic saltbush of the Rocky mountain plains. It is not so tolerant of alkali as most of the other species, some of which always replace it in strongly saline areas. It is a most valuable forage plant, surpassed in quality, but not in quantity, only by the following:

ATRIPLEX PABULARIS Aven Nelson, Bull. Torr. Bot. Club 25: 203.—The known range of this well marked species is being gradually extended. It has been found now in several of the saline districts of Wyoming and will no doubt be found elsewhere.

ATRIPLEX EREMICOLA G. E. O., Bull. Torr. Bot. Club 25:284, is very closely allied to the preceding, distinguished principally by a more branched, woody, and decumbent base.² It may have to take varietal or even lower rank.

ATRIPLEX EXPANSA Wats. Proc. Am. Acad. 9:116.—A very large part of the specimens found under this name are quite distinct from typical *A. expansa*. In the collections of the Missouri Botanical Garden only two were found to be true *A. expansa*, while there were several which are now named as below. The typical form apparently extends westward from New Mexico on either side of the "boundary." It is a much larger plant, "growing in intricately entangled masses 6-10 feet in diameter and 4-6 feet high." Stems and branches have fairly long internodes, the spikes interrupted, leafless toward the apex.

Atriplex philonitra, n. sp.—Annual, silvery-white, with a dense scurfiness, freely branched throughout, widely spreading and forming low tangled masses, 2-4 dm high: leaves in young plants from broadly ovate to orbicular, 3-nerved, 1-3 cm long, on petioles mostly exceeding the leaves; in older plants very numerous, rhombic-ovate or subcordate, on the branches becoming acute, gradually smaller and bract-like: monoecious, androgynous and also with unisexual clusters, floriferous and leafy-bracted throughout, the crowded clusters at the closely approximated nodes of the spike-like branches: calyx small, only the tips of the sepals free: anthers large: fruiting bracts suborbicular, about 5 mm broad, barely united above by the irregularly toothed narrow margins, the backs appendaged by short, thick, flat processes: radical superior.

This has heretofore been confused with the preceding, from which the three forms of flower clusters on the same plant, and the crowded bracteate spikes easily distinguish it. The axial branch of each plant is usually wholly staminate. Most of the specimens collected in the Rocky mountains north of New Mexico and ticketed *A. expansa* will be found to belong here. I make the type of the species my no. 8171, Laramie river, Wyoming, Sept. 1900.

ATRIPLEX ARGENTEA Nutt. Gen. 1:198.—*A. volutans* Aven Nel-

² For distinctions in seed (fruit) characters see "Seeds of commercial saltbushes," Bull. 27, U. S. Dept. of Agric., Div. of Bot.

son, Bull. Torr. Bot. Club 25:203.—In this species we have one of the most variable plants in respect to habit and size that has ever come under my observation. The original Nuttallian form is small and erect, but the large number of specimens at hand seem to furnish a complete series leading up to the other extreme represented by the large "tumble weed," often a meter in diameter, that was described as *A. volutans*. The distinctions as to the fruit characters are not sufficiently marked to maintain the latter as a species.³ Its polymorphism is correlated with its wide range.

ATRIPLEX POWELLII Wats. Proc. Am. Acad. 9:115.—Though this species is accredited to S. W. Colorado by Coulter's *Manual*, I am not sure that it rests upon any specimens except the type, which was grown under cultivation from seeds obtained from Arizona.

ATRIPLEX WOLFII Wats. Proc. Am. Acad. 9:112.—This excellent species is still quite rare in herbaria, all the specimens seen by me being from Colorado. Allied to it but quite distinct, as will be seen, is the following :

Atriplex tenuissima, n. sp.—Annual, branched from near the base, the slender branches racemosely branched into filiform branchlets, 2–3^{dm} high, moderately white-scurfy throughout: leaves numerous, bract-like, oblong to lance-ovate or broader, 1–7^{mm} long: floriferous from near the base; the few-flowered (1–3?) clusters axillary (pistillate plant the only one seen): fruiting bracts very small, mostly less than 2^{mm} long, triangular-ovate, completely united, forming a subpyramidal fruit irregularly and rather numerous tuberculate below the middle.

This proposed species is based upon a specimen in the Herbarium of the Missouri Botanical Garden, *M. E. Jones* 6525, Gunnison, Utah, Sept. 15, 1900, altitude about 1600^m. Distributed as *A. Wolfii*, to which it has some resemblance in habit, but the foliage and fruit are very distinct.

ATRIPLEX SACCARIA Wats. Proc. Am. Acad. 9:112.—During several years of collecting in southern Wyoming, nothing answering to this description has yet been encountered, in this the supposed type locality. It seems barely possible that the species rests upon one of the numerous variations of the following :

³ See Mr. G. N. Collin's valuable bulletin cited in the preceding footnote.

ATRIPLEX TRUNCATA (Torr.) Gray, Proc. Am. Acad. 8:398.—If this species, like *A. argentea*, be confined within the limits of the original description, it becomes quite local and meagerly represented. Several forms, differing among themselves as to habit and size, and even to some extent as to fruit characters, seem best to leave united with it. A year ago the writer marked some of these forms for specific rank, and (unfortunately) went so far as to distribute two of them with herbarium names, "*ined.*" The numbers so distributed are 8141 and 8170. Including these forms its range now seems to be from W. Nebraska to Oregon.

ATRIPLEX SUCKLEYANA (Torr.) Rydb. Mem. N. Y. Bot. Gard. 1:134.—The original range, "upper Missouri and head-waters of the Yellowstone," may have added to it "near the North Platte and some of its tributaries."

Atriplex spatiosa, n. sp.—A large erect annual, freely and divergently branched, often 1^m high, greenish-gray, minutely scurfy throughout: leaves ovate 2–5^{cm} long, coarsely and irregularly toothed, cuneate at base, rarely subhastate, nearly sessile, acute at apex with a minute cusp; the floral gradually reduced, becoming lanceolate and bract-like: monocious, androgynous at least above, the flowers in small axillary clusters and in ebracteate terminal spikes: calyx deeply 5-cleft: fruiting bracts small, rarely 5^{mm} long, ovate-triangular or orbicular, appressed, free above, with green border, hastately toothed near base or with several smaller teeth, the back crested with a semicircle (usually) of small slender green appendages.

This species came under my observation some three years ago, but the specimens secured happened to be found on loose banks and railroad grades, and it was suspected that it might be an introduction. It is proposed even now with some hesitation but with more confidence, since in the Herbarium of the Missouri Botanical Garden is found a specimen by *Dr. Vasey*, no. 487 (Powell's Colo. Expd. 1868), which undoubtedly is the same thing, though it was distributed as *Obione argentea*. Two others occur which are probably the same, namely, *Hayden*, Ft. Pierre, 1853; and *Hitchcock* 439, Kansas, 1895; these also as *A. argentea*. The relationship is nevertheless rather with *A. rosea* L.

The type number is 8140, Granger, Wyoming, Aug. 1900; *Elias Nelson* 737, Laramie, Wyoming, Sept. 1901, may be named as the co-type.

Atriplex carnosa, n. sp.—Annual, stout, branched, at length widely and diffusely so, sometimes nearly 1^m high: stems green, subglabrous: leaves thick and fleshy, oblong-lanceolate or broader, 3–7^{cm} long, on petioles less than half as long, mostly entire, the larger ones subhastate or with one or more large teeth near the base: fruiting spikes numerous, more or less paniced, at first dark green, becoming dark purple at maturity; the large fleshy clusters closely approximated, producing an almost continuous spike often 1^{cm} in diameter: fruiting bracts triangular-ovate, about 5^{mm} long and broad, usually one or more small teeth on the margins, smooth on the back or with one or two fleshy tubercles: radicle inferior or subascending.

This is a member of the *A. patula* group. *A. patula* does not occur in this region except as an introduction. Dr. Watson (Rev. N. A. Chenopodiaceae) states that the American form of *A. hastata* also differs somewhat from the European *A. hastata* L. It may of course at some time be separated. The other two varieties recognized by Watson are wholly distinct from the species now proposed, leaving only *A. lapathifolia* Rydb. Mem. N.Y. Bot. Gard. 7:133 with which to compare it. From this it seems to be distinct by its great fleshiness, its large spikes and lax habit, and hastately toothed leaves.

It occurs only in moist strongly alkali-impregnated soils, and seemingly extends from Nebraska across the middle Rocky mountains into Utah. The type is 8036, Laramie, Wyoming, 1900; wholly typical are 4465, Howell lakes, Wyoming, 1897; 1871, Laramie, Wyoming, 1895.

CHENOPODIUM.

Two years ago a very anomalous *Chenopodium* was discovered, growing in an alkali lake bed. The soil was moist, but the surface was covered with efflorescent salts. The plants were abundant and uniform in habit. The only known species that the plant suggested was *C. glaucum*. This led to an examination of *C. glaucum* and to further collections. After having seen many authentic specimens of both the introduced eastern form and the indigenous western form of *C. glaucum* there seems to be the best of reasons for designating this a new form as follows:

Chenopodium succosum, n. sp.—Stout, erect, 5–8^{dm} high, freely branched, the branches ascending or suberect, straw-

colored, the whole plant fleshy and exceedingly succulent (specimens curing slowly and saved with difficulty): leaves from broadly lanceolate to oblanceolate or even linear in outline, entire or irregularly toothed (often hastately toothed and resembling those of *Monolepis chenopodioides*), 2–5^{cm} long, on petioles about half as long, green on both sides and not noticeably mealy: floriferous throughout: flower clusters axillary, spicate, very numerous: calyx membranous; the sepals usually 3, suborbicular: pericarp thin, rather loosely covering the small dark brown seed.

It is at once distinguished from *C. glaucum* by its erect habit, size, succulence, greenness, crowded inflorescence, and small seeds. Type no. 8182a, Albany co., Wyoming, Sept. 5, 1900.

Chenopodium Watsoni, n. n.—*C. ^solidum* Wats. Proc. Am. Acad. 9:95, not *C. olidum* Curt. Fl. Lond. fasc. V. t. 20.

Chenopodium subglabrum (Wats.), n. sp.—*C. leptophyllum subglabrum* Wats. Proc. Am. Acad. 9:95.—The following characters seem to indicate that this rather rare plant is not very closely allied to *C. leptophyllum* Nutt. It is glabrous, usually bright green; loosely and slenderly branched, the branches very widely divaricate; the few-flowered clusters scattered on the branches. In this last respect especially it is as strongly marked as in its habit. The flowers are often borne singly and never more than two or three in a cluster. The fruit is large and depressed, and the calyx loose and open at maturity. Of several specimens examined in the herbarium of the Missouri Botanical Garden, no. 274, by Mr. Waugh, Stillwater, Oklahoma, shows the fully developed characters especially well. The range of the species seems to be from the Upper Platte in eastern Wyoming to Indian Territory.

In contrast with the preceding the var. *oblongifolium* of *C. leptophyllum* seems much less well marked. It is often difficult to say whether a given plant should bear the varietal or specific designation. Under this varietal name, however, a form has been found that by reason of its habit and other characters seems to deserve specific rank.

Chenopodium desiccatum, n. sp.—Annual, densely white mealy

throughout, freely branched, the branches paniculately branched, low and spreading, about 1^{dm} high (broader than high): leaves entire, from oblong to linear, mostly acute, some of them short petioled, 1–2^{cm} long: floriferous throughout; the small clusters in dense panicles which are naked towards the apex: calyx thickened with the dense mealiness, brittle, enclosing the fruit, the large (more than 1^{mm}) shining-black seed easily separable from the pericarp.

No. 5048, collected by *Elias Nelson*, Mill creek, Wyoming, Aug. 12, 1898 is made the type, while a collection by *J. H. Cowen*, Fort Collins, Colorado (wholly typical as represented in the Rocky Mountain Herbarium), July 29, 1896, may be designated the co-type.

Chenopodium cycloides, n. sp.—Annual, about 4^{dm} high, stoutish, divergently branched from near the base, nearly glabrous: leaves narrowly linear (the early ones wanting), 5–25^{mm} long, scattered on the branches or more crowded on slender branchlets, lightly scurfy on both sides: sepals 5, not scurfy, membranous, at maturity somewhat united and spreading, simulating a rotate wing about the large brown depressed or lenticular fruit: pericarp thin, close-fitting, transparent: seed more than 1^{mm} broad, embryo annular.

Of this seemingly remarkable distinct species I have seen but one collection, no. 435, by *A. S. Hitchcock*, Sand hills, Grant co., Kansas. It was distributed as *C. leptophyllum*, to which it is most nearly related, notwithstanding its very different appearance. The habit of the plant and its winged fruits at first sight suggest a *Cycloloma* rather than a *Chenopodium*. The type is the above number as it is found in the Herbarium of the Missouri Botanical Garden; the co-type, same number in the Rocky Mountain Herbarium.

DONDIA.

In the transfer of the different species from *Suaeda* to *Dondia*, there seems to have been some misunderstanding of the synonymy. Dr. Watson in his Revision (Proc. Am. Acad. 9: 87–90) seems to have had this perfectly clear, and there the synonymy may be found in full up to that date. The following new combinations seem to be necessary:

Dondia Moquini (Torr.), n. comb.—*Chenopodina Moquini* Torr. Pacif. R. R. Rep. 7: 18. 1856; *Suaeda Torreyana* Wats. Proc. Am.

Acad. 9:88, 1874; *Dondia multiflora* Heller, Cat. N. A. Pl. 3. 1898.

Dondia multiflora (Torr.), n. comb.—*Suaeda fruticosa multiflora* Torr. Pacif. R. R. Rept. 4:130. 1857; *S. suffrutescens* Wats. Proc. Am. Acad. 9:88. 1874; *Dondia suffrutescens* Heller, Cat. N. A. Pl. 3. 1898.

Dondia erecta (Wats.), n. sp.—*Suaeda depressa erecta* Wats. Proc. Am. Acad. 9:90. 1874; *Dondia depressa erecta* Heller, Cat. N. A. Pl. 3. 1898.

This is given specific rank, not because a depressed erect plant is an anomaly, but because by reason of its constant well marked habit it is quite distinct. Not only is it erect, but its narrow leaves and strict branches give it an aspect quite its own.

MISCELLANEOUS SPECIES.

Recently a specimen of *Abronia fragrans* Nutt. was received from T. D. A. Cockerell, of New Mexico. It seemed so different from the Wyoming form of that species that it led to an inquiry as to the typical *A. fragrans*. All the literature indicates a viscid pubescent plant, and that is just what we find in specimens secured to the southward and eastward of Wyoming. The Wyoming form, which seems to extend northward and westward, differs so essentially, it seems to me, that it may well bear a varietal name.

ABRONIA FRAGRANS glaucescens, n. var.—Growing in clumps, freely branched, suberect, 15–25^{dm} high: stems glabrous or nearly so below, upwardly becoming puberulent and subviscid: leaves wholly glabrous, light green above, lighter and more or less glaucous below (often silvery-glaucous): the white flowers crowded in the involucre and forming spherical clusters 5^{cm} or more in diameter (locally known as “snowballs”): fruit terminating in a conical beak one-third as long as the narrowly winged obconical body.

Abronia cheradophila, n. n.—*Abronia arenaria* Rydb. Mem. N. Y. Bot. Gard. 1:137; not *A. arenaria* Menzies, ex. Hook. Exot. Fl. t. 193.

Allionia glandulifera, n. sp.—Perennial from woody rootstocks: stems one or more from the crowns, somewhat dichotomously

branched, finely striate, silvery-glaucous below, greener upward and becoming glandular-pubescent, 3-5^{dm} high: leaves linear-lanceolate, mostly with one or more pairs of lateral nerves, obscurely undulate-toothed, glabrous or the uppermost viscid-pubescent, green and nearly normal in texture, 7-12^{cm} long, 5-10^{mm} broad: inflorescence a large freely branched cyme, nearly naked, densely viscid or glandular-pubescent throughout, even on the small bracts: involucre mostly three-flowered, salverform in anthesis, 1^{cm} or less in diameter, the bracts elliptic-ovate, sub-acute, distinct nearly to the base: perianth white or pinkish, broadly funnelform, 7-10^{mm} long, hirtellous without and within; its limb deeply four-lobed, each lobe bifid, giving eight subequal obtuse elliptic segments: stamens three, well exerted as also the style: fruits narrowly obovate, about 5^{mm} long, inconspicuously ribbed, somewhat tumidly rugose, moderately pubescent.

This is the Rocky mountain form of what has passed as *A. linearis* Pursh, but from that it is readily distinguished by its broader leaves of normal texture, its viscid-pubescent paniculate cyme, and the bifid lobes of the perianth.

ENOMEGRA.⁴—Coarse perennial herbs with thick milky (white) sap and alternate pinnate or bipinnate leaves; green or sometimes glaucescent but not blotched with white; densely hispid-spinescent on stem and capsules and more sparsely so on the toothed lobes of the leaves and on their veins; also a short puberulence which on the stem and especially on the capsules tends to become hispid. Flowers subsessile, in close clusters on the ends of the leafy simple stems. Sepals 3, hispid near the corneate, subcucullate apex, conspicuously reticulate veiny and inequilateral by the wing-like membranous margin on one side. Petals 4-6, white, suborbicular or reniform. Stamens numerous, filament and anther both narrow, sub-equal. Stigma dilated, four-lobed. Capsule cylindric-ellipsoid, four-valved. Seeds numerous, flattened, scarcely pitted. (Anagram of *Argemone*.)

This genus must rest mainly upon the color of the sap (no one seems to have made the observation that it is white), the character of the pubescence, the simple stems, and the crowded inflorescence. The glaucescent blotching

⁴This new genus unintentionally reached publication first in the writer's *Key to Rocky mountain flora* (1902), p. 27, but it seems best to give it this fuller additional publication.

with white in *Argemone* is noticeably absent in *Enomegra*. *Argemone intermedia* and *Enomegra bipinnatifida* are often associated in the field but are never confused. The veriest tyro distinguishes them almost as far as he can see them, as I have repeatedly proven. Even children before breaking them down say "yellow" (sap), "white," "yellow," "white," etc. Possibly the genus is monotypic but I rather suspect not. In either case some of the characters given above are specific rather than generic. Collectors too often make inadequate notes, and even in plants of this family the color of the sap is not mentioned. I have not collected personally the second of the species that follow.

Enomegra bipinnatifida*, n. comb.—Argemone bipinnatifida* Greene, Pitt. 3:346.

ENOMEGRA HISPIDA, Aven Nelson, *Key Rocky Mt. Fl.* 27.—*Argemone hispida* Gray, Pl. Fendl. 5.

***Draba uber*, n. sp.**—Stems several to many from a short branched caudex, moderately stout, 1–2 dm high (including the long fruiting racemes), lightly pubescent with mostly simple hairs: basal leaves densely rosulate on the crowns, oblanceolate, 1–2 cm long, tapering into a short petiole or subsessile, moderately stellate-pubescent as are also the stem leaves; stem leaves few, oblong, sessile but neither auriculate nor clasping: inflorescence crowded in fruit as well as in flower; flowers yellow, small: sepals subglabrous: petals spatulate, 4–6 mm long: fruiting from near the base up, the dense raceme leafless and ebracteate above the middle: pedicels stoutish, ascending, about 5 mm long: pods lanceolate, 10–12 mm long, puberulent with mostly simple hairs, 24–36-seeded, usually strongly twisted; style evident (1 mm), stoutish, glabrous.

In habit this species simulates *D. streptocarpa* Gray, but in some of the floral and fruit characters it is most nearly allied to *D. surculifera* Aven Nelson. From the latter it differs in the smaller leaves, long crowded fruiting raceme, narrower petals, more numerous seeds, and the denser and more uniform pubescence. *D. surculifera* occupies shaded slopes, under cliffs and trees in subalpine stations, while *D. uber* is found on open alpine slopes. Type no. 7875, Telephone mines, August 1, 1900.

***Lesquerella macrocarpa*, n. sp.**—Moderately stellate-pubescent throughout; freely branched from crown of a slender taproot; the branches decumbent-spreading with assurgent tips, 7–15 cm long: crown leaves from orbicular to obovate, 7–20 mm long,

mostly short petioled; stem leaves from broadly to narrowly oblong or oblanceolate, 15–30^{mm} long including the short tapering petiole: raceme crowded even in fruit, naked above: petals obovate, emarginate, two of them with slightly narrowed and claw-like base, 5–7^{mm} long: pod nearly globose, 5–8^{mm} in diameter, two or three ovules in each cell; style 2–3^{mm} long: pedicels recurved, 5–10^{mm} long.

This excellent species has the appearance of a *Physaria*, but of course is at once separated by the fruit. It was secured on naked clay flats and ridges on the Red desert, near the Bush ranch, Sweetwater co. Wyoming, June 10, 1900. The type number is 7081. It was again collected not far from the type locality in June 1901, by *Merrill* and *Wilcox*, no. 568.

Opulaster Ramaleyi, n. sp.—Shrubby, 1–2^m high; the stems and older branches brown with fibrous-shreddy bark; young branchlets green, glabrous and somewhat angled: leaves numerous and large, broadly ovate or subcordate in outline, some of them slightly incisely 3-lobed, the margin more or less doubly crenately dentate, 2–7^{cm} long and almost as broad, glabrous on both sides except occasionally some ciliolations on the veins below: pubescence on pedicels soft and rather long, somewhat tufted and substellate; on hypanthium and calyx short, hoary-tomentose: sepals ovate, acute, soon reflexed in blossom but erect in fruit, about 3^{mm} long: petals orbicular, slightly exceeding the sepals: anthers dark purple: ovaries four, loosely united to the middle, densely pubescent; carpels elliptic, inflated, more than twice as long as the sepals, about 7^{mm} long, moderately divergent, nearly distinct, pubescent, somewhat laterally compressed at apex and terminated by the short style, usually three maturing (sometimes only two): seeds single in the cells, obovoid, shining, about 2^{mm} long.

This is *O. opulifolius* probably, in so far as Rocky mountain specimens have been so named. It is not the *O. opulifolius* (L.) Kuntze of the eastern United States. The characters as given show that, and it is at once evident to the eye when both species are seen together. The type specimens are nos. 108, 793, and 874 by *Francis Ramaley*, all from the same locality, near Boulder, Colorado, 1900 and 1901. The earlier number is in blossom, the two later in fruit. No. 2406 by *G. E. Osterhout*, 1901, is the same and from the same locality.

Anogra Nuttallii, n. comb.—*Oenothera albicaulis* Nutt. Fras. Cat., name only; T. & G. Fl. N. A. 1:495; not Pursh, Fl. Am. Sept. 733; *O. Nuttallii* Sweet, Hort. Brit. Ed. 2:199.—Perennial from woody horizontal rootstocks with short vertical caudices or crowns: stems one to several from the crown, erect, 5–10^{dm} high, freely branched above, the somewhat shreddy bark white and glistening; branchlets slender, widely divaricate: leaves very numerous, somewhat fascicled at the axis, softly and minutely puberulent on the lower surface, broadly linear, acute at apex, tapering gradually to the nearly sessile base, margin entire or merely denticulate; the primary ones of the fascicles 4–10^{cm} long, 5–8^{mm} broad; the secondary ones similar but quite small: flowers in the crowded terminal axils of the branches, somewhat drooping in bud: calyx glandular-puberulent on the tube; calyx-lobes narrowly lanceolate, 2–3^{cm} long, about as long as the tube, scarcely puberulent, the tips free: petals white, broadly obovate, entire or denticulate at the broad apex, nearly as long as the reflexed calyx-lobes: anthers linear, 15^{mm} long, as long as the filament: stigmas exserted, linear, about 10^{mm} long: mature capsule cylindrical, about 3^{cm} long, pale, minutely puberulent except on the rather broad whitish sutures, not contorted: seeds narrowly ovate, light green, copiously speckled with purple, indistinctly striate under a lens, about 2^{mm} long.

I have long intended to give a name to this perfectly valid species. In fact I have distributed some specimens under the herbarium name *Anogra arenaria*. A more careful study of the synonymy convinces me now that the above name is tenable. *Oenothera albicaulis* Nutt. never was a synonym of *O. pallida* Lindl. Bot. Reg. 14: pl. 1142. It was evidently the purpose of Sweet to distinguish this species of Nuttall from Pursh's species of the same name, as it was also of Spach in his *Baumannia Nuttalliana* (Hist. Veg. 4: 352) and *Anogra Nuttalliana* (Nouv. Ann. Mus. Par. 4: 339).

This species is very common on sandy plains and banks from Nebraska to Utah. It is at once distinguishable from *Anogra pallida* by the pubescent leaves, inflorescence, and capsules; the larger flowers (resembling those of *A. albicaulis* Pursh rather than those of *A. pallida*), and the larger straight capsules and characteristic seeds.

Lavauxia Howardi (Jones), n. comb.—*Oenothera Howardi* Jones, Zoe 3: 301.—For some reason this species has been completely ignored by recent writers on the allies of *Oenothera*, as

has also *Oenothera Johnsoni* Parry, Am. Naturalist 9: 270. Jones suggests the possibility that the species he describes is *O. Johnsoni*, but at the same time points out characters that unmistakably distinguish the two. While the description of *O. Johnsoni* is very meager, yet in so essential a matter as the character of the capsule it is very explicit. Certainly no observer, least of all Parry, would have compared a large perennial such as *Lavauxia Howardi* with the small annual *Lavauxia primumervis* (Gray) Small, which has a capsule similar to that attributed to *O. Johnsoni*. The species to which *Lavauxia Howardi* is closely allied is *L. brachycarpa* (Gray) Britton Mem. Torr. Club 5: 235; *Oenothera brachycarpa* Gray, Pl. Wright 1: 70, and Coulter, Contrib. U. S. Nat. Herb. 2: 116; but here again the character of the capsule serves to distinguish these two. In the latter it is smooth and acute, with narrow wings; while in the former it is larger, oblong-obtuse, broadly winged, and cinereous pubescent. The leaves also are all oblanceolate, tapering into the petiole, from entire to coarsely and irregularly toothed, therefore the lamina continuous and not distinguished into lateral and terminal lobes.

The species occurs on arid denudated hills from northern Colorado through Utah to Nevada.

COLORADO AND WYOMING THORNS.

Crataegus Wheeleri, n. sp.—Probably a small shrub, the branches slender and virgate: leaves narrowly oblong to elliptic, 3–5^{cm} long, 1–2^{cm} broad, from acute to obtusely rounded at apex, cuneately tapering at base to a slender petiole one-fourth to one-half as long as the blade, the shallow crenate serratures wanting on the cuneate base, light green and glabrous below, brighter green but obscurely and sparsely appressed strigulose above, firmer in texture and somewhat glossy above at maturity: spines slender, flexible, glossy black, 2–3^{cm} long: flowers small, 12–14^{mm} broad, on slender glabrous pedicels, in close few-flowered corymbs: calyx-tube obconic, glabrous; calyx-lobes small, triangular, at length reflexed: petals suborbicular, about 4^{mm} in diameter: stamens 20; anthers yellowish-white: pistils 5: fruit small, sub-globose, 6–8^{mm} in diameter, purplish-black (in dried specimens), in few-fruited suberect clusters; flesh seem-

ingly very thin and dry: nutlets 5, nearly smooth, about 5^{mm} long.

This species is not so well represented before me as I wish it were, but it is so evidently distinct from the known Rocky mountain species that I have no hesitancy in pronouncing it new. Among the western species it is most nearly allied to *C. rivularis* Nutt. The size of the tree or shrub is not known to me, but from the herbarium specimens I suspect that it is quite small. The type was collected by *H. N. Wheeler* at Sapinero, Colorado, 1898, no. 532; co-type, *C. S. Crandall's* collection in the Black cañon of the Gunnison, Colorado, August 22, 1896.

Cartaegus cerronis, n. sp.—Tree-like in form, 2–5^m high, rather widely branched; trunk short and stout, with rough bark; young twigs brown, passing into the gray of the older ones; lenticels small, nearly white: leaves broadly elliptic-ovate, 3–5^{cm} long, 2–3^{cm} broad, coarsely and serrately few-toothed, the teeth with finer gland-tipped acute serrations, acute or acuminate at apex, the abruptly cuneate base entire or remotely serrulate, light green and perfectly glabrous below, sparsely ciliate pubescent above, especially on the veins; petiole slender, without glands, channeled above, 5–20^{mm} long: thorns numerous, short (2–3^{cm}), stout and thick for the length, straight, rarely a little deflexed, very dark morocco-red, with small light-covered lenticels: the paniculate corymb 5–10-flowered, congested in blossom but more open in fruit: calyx tube only 2–3^{mm} long, shorter than its lobes; lobes ovate, with a broad gland-margined acumination: petals suborbicular, with shallow crenations, noticeably reticulate veined, 6–8^{mm} broad: stamens few (1–8, mostly 5–8); anthers large, purple: pistils 5: mature fruit not at hand; nutlets 5.

This excellent species seems to be an inhabitant of Colorado and Wyoming. I take as the type *Baker's* no. 46, Cerro summit, Colorado (altitude about 2500^m), flowers June 7, fruit July 12, 1901; excellent flowering specimens, 660 *Ramaley*, near Boulder, Colorado, May 20, 1901. The following numbers from Wyoming, by the writer, are probably the same, though only fruiting specimens are at hand: 2491, Pass creek, 1896; 606, Casper, 1894; also 5060, by *E. Nelson*, Seminole mts., 1898. It has probably at times been distributed as *C. rivularis* Nutt., but it has rather the appearance of *C. Douglasii* Lindl.

Crataegus sheridana, n. sp.—Becoming a small tree 3–5^m high; the young twigs gloss-brown or red-brown, becoming

grayish on older branches; lenticels rather few and large; spines slender, noticeably curved and deflexed, 4-5^{cm} long, dark brown, the glazed surface marked by the few whitish lenticels: leaves oval to almost orbicular, coarsely and incisely toothed with rather blunt gland-tipped serratures, the rounded or abruptly cuneately-narrowed base merely serrate and scarcely decurrent upon the slender petiole; pubescence various, sparse and softly strigose on lower surface of leaves (mostly on the veins), minute and appressed on the upper, ciliate on the petioles, the youngest twigs, the pedicels, the calices, and fruits: corymb 5-11 flowered: calyx-lobes ovate-lanceolate, with several glands on the margins, 4-5^{mm} long: stamens (seemingly) 8-10: pistils 3 or 4: nutlets 3-5, often slightly crested-bisulcate dorsally, about 5^{mm} long: fruit nearly spherical, 8-9^{mm} in diameter, scarlet-red.

The *Crataegus* here described has passed for *C. macrantha* Lodd. While it may be most nearly allied to that it is doubtful if anything referable to that species occurs in the Rocky mountains. Another close ally of it is found in *C. Piperi* Britt., from which it differs in pubescence, the absence of glands on the petioles, in the straight styles; the shorter filaments, and the smaller differently colored fruits.

The type is no. 8673, Sheridan, Wyoming, July 24, 1901; fully ripe fruits from same locality October, 1902. Sundance, Wyoming, July 2, 1896, no. 2104, seems to be the same.

UNIVERSITY OF WYOMING,
Laramie.

BRIEFER ARTICLES

A NEW HEPATIC FROM THE EASTERN UNITED STATES.

(WITH PLATE XII)

ALTHOUGH the species of *Diplophyllia* described below is not uncommon along the Atlantic coast, and has long been known to hepaticologists, it has been confused with other members of the genus. As the synonymy shows, Sullivant referred the plant to *Jungermannia obtusifolia* Hook., now known as *Diplophyllia obtusifolia* Trevis. This distinct species is widely distributed in Europe and has recently been reported by Stephani from Japan.¹ The only American station, however, which can be quoted with any degree of certainty is Hector, British Columbia, where it was collected in 1889 by Macoun and distributed in *Canadian Hepaticae*, no. 100. Austin threw doubts upon Sullivant's determination of the eastern plant, but instead of recognizing in it a distinct species referred it as a forma *minor* to his *Scapania albicans*, var. *taxifolia*. Nearly every writer on the Hepaticae now regards this so-called variety as a species distinct from *Diplophyllia albicans* (L.) Trevis., and it appears in recent literature as *D. taxifolia* (Wahl.) Trevis. With regard to the exact status of Austin's var. *taxifolia minor*, no views have recently been expressed except those of Pearson,² who apparently accepts the old determination of Sullivant.

Diplophyllia apiculata, sp. nov. — *Jungermannia obtusifolia* Sull., Gray's Manual, Ed. 1, 694. 1848 (not Hooker). *Scapania albicans*, var. *taxifolia minor* Aust. Hep. Bor.-Amer. 23. 1873.—Yellowish-green, more or less tinged with brown or red, growing in depressed mats: axes 0.17^{mm} in diameter, sparingly pinnate, both primary and secondary prostrate at the base and ascending toward the apex, with abundant pale rhizoids in the prostrate portions: leaves imbricated, deeply and unequally complicate-bilobed; antical lobe erect-spreading, ovate, 0.4^{mm} long, 0.2^{mm} wide, slightly narrowed at the base and attached by an almost transverse line of insertion, not decurrent, apex varying from rounded to subacute, mostly apiculate, margin entire or indistinctly and irregularly denticulate; keel slightly concave; postical

¹ Bull. Herb. Boissier 5: 78. 1897.

² Hepaticae of the British Isles, 242. 1900.

lobe falcate, linguiform, 0.75^{mm} long, 0.3^{mm} wide, scarcely narrowed at the almost transverse base, apex obtuse to subacute and usually apiculate, the apiculum consisting of one or two cells, margin subentire or sparingly and irregularly denticulate, especially toward the base, occasionally with one or more coarser teeth near the apex, postical margin usually forming a distinct but wide angle with the keel; cells of lobes isodiametric in apical region and along free margin, 12μ in diameter at the apex, $18 \times 12\mu$ in the middle, and $32 \times 12\mu$ at the base and along keel, cell-walls somewhat thickened, the thickening more or less uniform but with evident trigones in the median and basal portions of the lobes, cuticle varying from densely and finely verruculose to nearly smooth: inflorescence autoicous: ♀ inflorescence usually on a short branch, more rarely on an elongated branch, sometimes innovating on one or on both sides, commonly without innovation; leaves increasing rapidly in size toward perianth; bracts mostly in two or three pairs, similar to the leaves, their lobes obtuse to rounded but usually apiculate at the apex, antical lobe 0.85^{mm} long, 0.35^{mm} wide, postical lobe 1.2^{mm} long, 0.45^{mm} wide; perianth about one-third exserted, obovoid, 1.4^{mm} long, 0.7^{mm} wide, narrowed toward the base, somewhat constricted at the mouth, slightly compressed and with four to six grooves in the upper part, separated by rounded keels, mouth irregularly lacerate with setulose divisions, the ultimate setae sharp, one to three cells long: ♂ inflorescence borne on a leading branch, more rarely on a short branch, often proliferating at the apex and again floriferous; bracts in two or three pairs, similar to the leaves but with a strongly convex keel, antical lobe broad, inflated at the base; antheridia borne singly; paraphyses wanting: capsule oval, reddish-brown, borne on a slender stalk; spores 13μ in diameter, yellowish, minutely verruculose: gemmae borne in irregular masses at the apices of the upper leaves of a branch, composed of one or two angular cells.

On shaded banks. RHODE ISLAND: Providence and Exeter (*Collins*). CONNECTICUT: Killingworth (*Hall*); Woodbridge and Hamden (*Eaton*); Orange (*Evans*). PENNSYLVANIA: Philadelphia (*James*). DISTRICT OF COLUMBIA (*Holzinger*). VIRGINIA: Comer creek (*Mrs. Britton and Miss Vail*). GEORGIA: Tallulah falls (*Underwood*). The specimens from Orange, Conn., in the herbarium of the writer, may be designated as the type.

EXSIC.: *Musc. Alleg.* 230 (as *Jungermannia obtusifolia*); *Hep. Bor.-Amer.* 23 (as *Scapania albicans*, var. *taxifolia minor*).

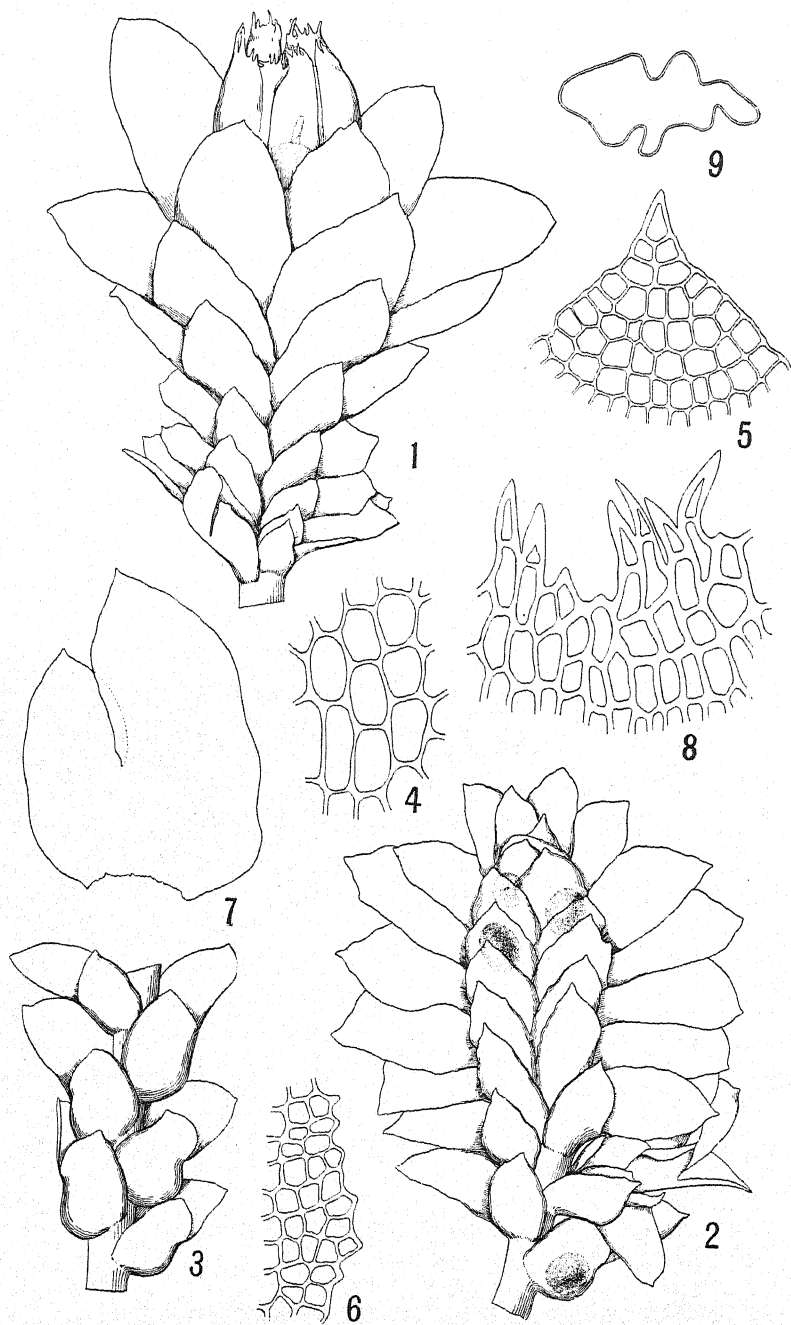
Whether the inflorescence of *D. apiculata* is invariably autoicous or whether it may sometimes be dioicous is difficult to determine, since it

is not always possible to demonstrate the connection between the male and female axes. This is especially true of plants with fully developed perianths, because the short female branches very early root at the base, lose their connection with the parent axes and continue their development independently. In plants with young perianths, however, and more particularly in those with unfertilized archegonia, the connection between male and female branches is usually clear and apparently indicates the normal condition of the species. The fact that a male axis sometimes proliferates at the apex and bears several successive male inflorescences without branching might seem to indicate that the species was on the way to becoming dioicous. Such a male branch indeed becomes eventually a distinct unisexual individual from the dying away of its older portions. Nevertheless, the occurrence of male individuals in a monoicous species is by no means unusual and is apparently brought about in some cases by unfavorable conditions.

The new species is related to *D. taxifolia* and also to *D. obtusifolia* and is in some respects intermediate between them. It is a smaller plant than *D. taxifolia* and differs from it also in its apiculate leaves and in its inflorescence, which is autoicous instead of dioicous. *D. taxifolia*,³ moreover, occurs usually on shaded rocks, while the new species prefers earthy banks. *D. apiculata* agrees with *D. obtusifolia* in its size and also in its place of growth, but differs from it in its apiculate leaves and bracts and in being autoicous instead of paroicous. *D. obtusifolia*, to be sure, occasionally produces branches which are purely male, but these occur on the same individuals or at any rate in the same tufts as bisexual branches, and the latter are undoubtedly the more typical. Another close relative of *D. apiculata* is *Diplophyllum gymnostomophilum* Kaalaas³ of Norway and Sweden. This species is dioicous, the male and female plants growing in distinct tufts. The Italian *Diplophyllia scapanioides* Massal.,⁴ a near ally of the Scandinavian species, is also dioicous.—ALEXANDER W. EVANS, *Yale University*.

³*Scapania gymnostomophila* Kaalaas, Bot. Notiser 1896: 21. *Martinellia gymnostomophila* Arnell & Jensen, Bihang till K. Sv. Vet.-Akad. Handl. 21^{no}: 28. pl. — f. B. 1896. *Diplophyllum gymnostomophilum* Kaalaas, Vidensk. Skrift. I. 1898^o: 4-9. f. 1-4.

⁴*Jungermannia scapanioides* Massal. Acta Soc. Ven.-Trent. 6: [64]. pl. 3. 1879. *Diplophyllia scapanioides* Massal. Ann. dell' Ist. Bot. di Roma 2^a: [18]. 1886. See also C. Müller (Freiburg), Bot. Centralblatt 82: 411. 1900.



DIPLOPHYLLIA APICULATA Evans

EXPLANATION OF PLATE XII.

- FIG. 1. Branch with perianth, antical view. $\times 36$.
FIG. 2. Branch with δ inflorescence, antical view. $\times 48$.
FIG. 3. Branch with old perigonial bracts. $\times 48$.
FIG. 4. Cells from middle of postical lobe. $\times 420$.
FIG. 5. Cells from apex of same. $\times 300$.
FIG. 6. Cells from margin of same near base. $\times 300$.
FIG. 7. Perichaetial bract. $\times 48$.
FIG. 8. Teeth from mouth of perianth. $\times 300$.
FIG. 9. Cross-section of perianth in upper third. $\times 48$.
The figures are all drawn from the type-specimens.

CURRENT LITERATURE.

MINOR NOTICES.

C. H. ROBISON, instructor in biology in the high school of Oak Park, Illinois, has published a pamphlet entitled "Outlines for field studies of common plants" that deserves attention. It is the result of a large and successful experience in such work with pupils of high school age. The price is 25 cents, and copies can be obtained by addressing the author.—J. M. C.

W. L. JEPSON² has published a school flora for the Pacific coast, a companion book to Nelson's *Key to Rocky mountain flora* and Coulter's *Analytical key to flowering plants* for the northeastern states. Of all these areas perhaps Professor Jepson's was the most difficult to treat in the selective way, since it comprises three very dissimilar botanical regions. However, no one is better fitted to have made this selection than the author, and the descriptions show the great personal familiarity of the field student.—J. M. C.

THE SEVENTH PART of the *Catalogue of Canadian plants* has just appeared. The sixth part was published in 1892, and contained a list of the Canadian mosses. The present part contains the liverworts and lichens. The liverworts number 196 species, and the lichens 614. An extensive "Addendum to Part VI" (138 pp.) is also published, bringing up to date "our knowledge of American mosses north of the United States." Professor Macoun is to be congratulated upon the persistent way in which this very valuable catalogue is being pushed to its completion.—J. M. C.

THE VOLUME OF the *Proceedings of the Indiana Academy of Science* for 1901, just issued, contains the following botanical papers: Flora of Eagle lake and vicinity, by H. W. CLARK; The vegetation of abandoned rock quarries, by MEL T. COOK; Contributions to the flora of Indiana, by STANLEY COULTER; Effect of the composition of the soil upon the minute structure of plants, by H. B. DORNER; Correlation of forestry and the sciences, by W. H. FREEMAN; A study of the histology of the wood of certain species of pines, by KATHERINE E. GOLDEN; The germinative power of the conidia of *Aspergillus Oryzae*, by MARY F. HILLER; A collection of myxomycetes, by F. MUTCHLER; Spore resistance of loose smut of wheat to formalin and hot water, and Some additions to the flora of Indiana, by WILLIAM STUART; Forestry in Indiana (Presidential address), by M. B.

²JEPSON, WILLIS LINN, A school flora for the Pacific coast. vi + 96. New York: D. Appleton and Company. 1902.

THOMAS; Notes on apple rusts, and Notes on the genus *Stemonitis*, by H. H. WHETZEL; The plant ecology of Winona lake, by LUCY YOUSE. The secretary of the Academy is John S. Wright, Indianapolis, Ind.—J. M. C.

NOTES FOR STUDENTS.

STUDENTS OF STEM ANATOMY will be interested in a recent paper of Solms-Laubach² upon the branching of *Isoetes lacustris*. The occurrence of a large number of branching specimens of unusual luxuriance and size, in a lake visited by the author in 1897, led him to a detailed study of the stem and a review of the literature upon the subject.—FLORENCE M. LYON.

TOBLER³ finds that the thallus of one of the Rhodomelaceae, namely *Dasya elegans*, breaks down into single cells and cell-groups under certain conditions, and that these cells retain their vitality and finally develop new thalli, after the manner of the process which occurs so often in the Conjugatae and Confervoideae. The exact conditions under which this breaking down occurs were not worked out, but the author is sure the active stimulus is not one of increase in concentration of the external solution.

Observation that the ultimate branches of *Bryopsis plumosa* fall off and exhibit a marked power of growth somewhat similar to that just described, and that they sometimes form long siphonaceous tubes much resembling those of *Vaucheria*, has been made by Wright⁴ and recorded in a recent note.—B. E. LIVINGSTON.

TWO FUNGUS DISEASES of the white cedar (*Cupressus thyoides*) are described in a recent paper by Harshberger.⁵ These are caused by *Gymnosporangium biseptatum* Ellis, and *G. Ellisii* (Berk.) Farlow, both of which grow in the wood of the cedar. The author discusses the normal structure of the cedar wood, paying special attention to the number of tracheids in the various annual rings, and the conditions which influence their development. The influence of the growth of the fungus mycelia in the stems is evidenced by the formation of swellings, which show a large increase in the number of tracheids and increased activity of the phellogen. In the swellings caused by *G. biseptatum*, many of the tracheids appear to be plugged by a substance which the author calls "fungus gamboge." A detailed description of the structure of the swellings, the mycelia, and a consideration of the relation of the host cells and the hyphae follow.—H. VON SCHRENK.

²SOLMS-LAUBACH, H. GRAF ZU, *Isoetes lacustris*, seine Verzweigung und sein Vorkommen in den Seen des Schwarzwaldes und der Vogesen. Bot. Zeit. 60:179-206. pl. 7. 1902.

³TOBLER, F., Zerfall und Reproduktionsvermögen des Thallus einer Rhodomelaceae. Ber. Deutsch. Bot. Gesell. 20:357-365. 1902.

⁴WRIGHT, E. P., Note on *Bryopsis plumosa*. Notes from Bot. School Trin. Coll. Dublin. 1:174-175. 1902.

⁵HARSHBERGER, JOHN W., Two fungus diseases of the white cedar. Proc. Acad. Nat. Sci. Philadelphia, 1902: 461.

A NEW SUGGESTION as to the nature and origin of protoplasm has been made by Herrera.⁶ By triturating the acetate, carbonate, or chlorid of calcium with glacial phosphoric acid, and then treating the resulting substance with salt solutions, the author obtains a mass which behaves under the microscope very much as does protoplasm. It shows amoeboid motion, a vacuolar or granular structure, plasmolyzes in certain cases when treated with plasmolyzing solutions, can be stained with methyl green, has its movements accelerated by sodium chlorid, etc. Herrera ventures the tentative hypothesis that "natural protoplasm is an inorganic metaphosphate impregnated by various substances absorbed or secreted under special osmotic and electric conditions." From the standpoint of such an hypothesis the theoretical explanation of the first appearance of the living substance upon the earth might not be such a difficult problem as it has heretofore seemed.—B. E. LIVINGSTON.

IN A PRELIMINARY NOTE Kuckuck⁷ describes the phenomenon of zoospore production in *Valonia ovalis*. Parts of the protoplasm contained in the one-celled, bulbous thallus divide into zoospores, which escape through several openings produced by an apparent local absorption of the cell wall. After the escape of the zoospores these openings close and the remaining protoplasm occupies the entire cell, which resumes its normal vegetative appearance and continues the normal life processes. This is a case where during a very active period the protoplasm exists perfectly free from the conditions of turgor, so important at all times in most plant organisms; during the escape of the zoospores the large vacuole of the cell is in direct connection with the external solution through the several openings. Another curious fact is that the reproductive portion of the plasma is not separated by a wall from the vegetative part. In this respect *Valonia* differs from the other forms of the Siphoneae which have been studied; in them either the whole cell takes part in zoospore production and thus ends its career (*Botrydium*), or the portion so taking part is cut off from the rest by a wall formed previous to the actual division into zoospores (*Codium*, *Bryopsis*, *Vaucheria*).—B. E. LIVINGSTON.

IN A CONTINUATION of his studies on the lichens, Baur⁸ makes valuable additions to our knowledge of the development of the apothecia in a number of genera, and a résumé is given of the evidence for the sexuality of the lichens. The ascogons and trichogynes of *Parmelia* and *Pertusaria* are specially described and figured. Particularly interesting are Baur's observa-

⁶ HERRERA, A. L., Le protoplasma de métaphosphate de chaux. Mem. Rev. Soc. Sci. "Antonio Alzate," Mexico 17:201-213. 1902.

⁷ KUCKUCK, P., Zur Fortpflanzung von *Valonia* Gin. Ber. Deutsch. Bot. Gesell. 20:355-357. 1902.

⁸ BAUR, E., Die Anlage und Entwicklung einiger Flechtenapothecien. Flora. 88:319-332. pls. 14-15. 1901.

tions on *Pertusaria communis*. Krabbe who studied the same lichen states that he found no trace of sexual organs or of a differentiation of ascogons and paraphyses. Baur's sections show the characteristic thick, coiled ascogons and trichogynes and the later developed ascogenous hyphae most sharply differentiated from the surrounding vegetative tissue from which arise the paraphyses. Of special interest in this lichen is the capacity for indefinite development shown by the ascogenous hyphae. Growing and branching richly at their tips and dying off at their basal ends as they advance, they spread through the thallus and form apothecia at various points, even 2^{mm} distant from the original trichogyne and ascogon from which they arose. Such extended independent growth of the ascogenous hyphae forms a good parallel to what Watnio has already claimed for *Cladonia*. Baur also describes the development of the pyrenolichen *Pyrenula nitida*, and finds here also the characteristic differentiation of ascogon and trichogyne. The recent work of Baur and others has made the morphology of the ascocarp for the entire family of the lichens better known than it is in any other similar series of Discomycetes.—R. A. HARPER.

SINCE THE APPEARANCE of Czapek's answer to Wachtel's paper on the method of bent tubes to demonstrate the sensitiveness of root-tips to the gravity stimulus, we have had a desire for some entirely different method by which this long-discussed question could be attacked anew. Czapek's position seemed to be established, but the lack of confirmatory evidence from other sources has been still noticeable. In a recent paper by Francis Darwin⁹ a new method of approach is described. It is a modification of that used by him¹⁰ in showing that the cotyledon of *Setaria*, *Sorghum*, etc., is the perceptive region in geotropic curvature of the hypocotyl. Since the root tip is slimy and the whole organ mechanically weak, it is impossible to fix the tip in a horizontal tube and have it support the weight of the rest of the seedling. The new method obviates this difficulty by affixing the cotyledons to the end of a long lever free to move in both a vertical and horizontal plane. The lever is of course counterbalanced, and thus the cotyledons (of beans in this case) are able to move freely in any direction in a spherical plane, whose radius of curvature is the length of the supporting lever-arm. When the cotyledons are so supported the root-tip is placed in a horizontal tube (of straw, dandelion scape, etc.), and complete turns are executed by the curving root. The method is difficult of operation, and a large number of experiments failed because the root-tip slipped from the tubes. But the author believes he has demonstrated in this way that as long as the tip is horizontal the response of the growing region produces a continuous curve resulting in

⁹ DARWIN, F., On a method of investigating the gravitational sensitiveness of root-tip. Jour. Linn. Soc. 35:266-274. figs. 1-10. 1902.

¹⁰ DARWIN, F., On geotropism and the localization of the sensitive region. Ann. Bot. 13:567-574. pl. 29. 1899.

a spiral like those produced by similar treatment in the hypocotyls of grass seedlings.—B. E. LIVINGSTON.

THE ALMOST HOPELESSLY complex chemical changes which are constantly taking place during the life of the organism are gradually beginning to yield to modern methods of experimentation. Recently two papers have appeared on the transformations occurring in phosphorus compounds during germination, one by Iwanow¹¹, the other by Zaleski¹².

The former used seedlings of *Vicia sativa* grown in phosphorus-free Knop's solution, and determined the amounts of the various phosphorus compounds at the beginning of the cultures and after 5, 10, 15, 20, and 25 days. Determination was made (1) of total phosphorus content, (2) of inorganic phosphorus, (3) of the phosphorus or lecethin, (4) of the phosphorus of proteid compounds, and (5) of that of soluble organic compounds. Zaleski used seedlings of *Lupinus angustifolius*, grown in phosphorus-free sand, and determined the phosphorus (in the same categories of compounds as those determined by Iwanow) at the beginning of the cultures and after 10, 15, and 25 days. Both authors find that during germination inorganic phosphates increase at the expense of organic phosphorus compounds. Iwanow presents evidence that most of this phosphorus comes from the breaking down of phosphorus-containing proteids; some is from the soluble organic bodies bearing phosphorus, and a very little arises from the decomposition of lecethin. Zaleski determined that the decrease in organic phosphorus is mainly in the cotyledons, while the most marked increase in inorganic phosphorus is in the axial organs. He shows also that young and vigorous tips of seedlings of *Vicia faba*, placed in glucose solution, exhibit a less marked decrease in organic phosphorus compounds, as well as less rapid growth, than when these are placed in water. He concludes that the sugar retards both growth and the process of phosphorus-transformation, and that therefore it is possible to suppose a direct relation to exist between the breaking down of organic phosphorus-containing bodies and growth itself.—B. E. LIVINGSTON.

BURKILL¹³ has investigated the variation in the floral organs of *Ranunculus arvensis*. From a study of about 7,000 flowers, from seed obtained at Kew, England, and at Bonn and Heidelberg, Germany, he reaches essentially the following conclusions: Each set of floral organs varies according to a law of its own, and none of the curves agrees perfectly with any theoretical probability curve. Although the different whorls respond differently to conditions of favorable or unfavorable nutrition, there is always an apportionment

¹¹ IWANOW, L., Ueber die Umwandlungen des Phosphors beim Keimen der Wicke. Ber. Deutsch. Bot. Gesell. 20: 366-372. 1902.

¹² ZALESKI, W., Beiträge zur Verwandlung des Eiweiss phosphors in den Pflanzen. Ber. Deutsch. Bot. Gesell. 20: 426-433. 1902.

¹³ BURKILL, I. H., On the variation of the flower of *Ranunculus arvensis*. Jour. Asiatic Soc. Bengal 71:93-120. 1902.

of the available nutrition to the four sets of organs, no set ever being omitted because of the low vitality. If one set of organs is abnormal, all the other sets are likely to be abnormal, but especially the sets which follow. There is a gradual loss of vigor from beginning to end of the flowering period, though a slight recovery just before death was occasionally observed. Of all the floral organs the stamens are most influenced numerically by the relative vigor of the branch, the number being proportionately greater or less according as the whole number of floral parts is above or below the mode. As a result of this greater sensitiveness of the androecium, the flowers are relatively more staminate at the beginning of the flowering season than at any time thereafter. The degrees of constancy in the several sets of organs, beginning with the highest, are in the order: sepals, petals, carpels, stamens. A parallel is drawn between this condition and the relation of these parts to the natural classification, in which it is pointed out that sepals tend to be constant in number through the larger subdivisions of the Spermatophytes, petals in lesser divisions, carpels in the families, and that stamens are so inconstant as to be of little use numerically in a natural classification. The paper is a valuable contribution to our knowledge of floral variation, but the discussions of the problem and the interpretation of the results are rendered vague, and at times incomprehensible, by a diction which constantly suggests the possession of psychic attributes by the various organs or sets of organs.—G. H. SHULL.

ITEMS OF TAXONOMIC INTEREST are as follows: ARTHUR HOLLICK (Torreya 2: 145-148. pls. 3-4. 1902) has described a new species of fossil ferns from the Laramie group of Colorado in *Anemia* (2), *Acrostichum*, *Polystichum*, *Gleichenia*, and *Stenopteris*.—T. D. A. COCKERELL (*idem* 154) has described a new *Astragalus* from New Mexico.—C. V. PIPER (Bull. Torr. Bot. Club 29: 535-549. 1902), in discussing the biennial and perennial west American species of *Lappula*, has described 9 new species.—V. S. WHITE (*idem* 550-563), in giving a preliminary list of fungi from Bar Harbor, Mount Desert, Maine, has published new species of *Hydnum* (2) by H. J. BANKER, and of *Boletus*, *Clitocybe*, *Cortinarius*, and *Flammula* by C. H. PECK.—J. S. COTTON (*idem* 573-574) has described new species of *Glyceria*, *Astragalus*, and *Orthocarpus* from Washington.—G. F. ATKINSON (Jour. Mycol. 8: 106-107. 1902) has described two new genera of Basidiomycetes under the names *Tremellodendron* (Tremellineae) and *Eocronartium* (Auriculariaceae), and also (*idem* 110-119) 23 new species distributed among 16 genera.—G. P. CLINTON (*idem* 128-156) has published in preliminary form the results of his studies of North American *Ustilagineae*, presenting a list of the species with their hosts and distribution, and including descriptions of new species.—H. CHRIST (Bull. Acad. Internat. Geog. Bot. 11: 189-274. 1902), in giving an account of the Chinese ferns collected by Père Bodinier, under the title *Filices Bodinierianae*, has described new species of *Antrophytum*, *Polypo-*

dium (4), Nipholobolus, Adiantum, Doryopteris, Blechnum, Asplenium (3), Aspidium (4), Polystichum (5), and Gleichenia; the same author (Bull. Herb. Boiss. II. 2: 825-832. 1902), in reporting concerning the collection of Père Faurie (*Filices Faurieanae*) from Korea, has described new species of Athyrium (2) and Aspidium.—C. L. POLLARD (Proc. Biol. Soc. Washington 15: 201-203. 1902) has described two new violets from the eastern United States.—MARCUS E. JONES (Contr. to Western Bot. no. 10) has published a revision of Allium as represented in the Great Basin and adjoining regions, including 3 new species; has presented the Nyctaginaceae of the Great Plateau, including new species of Boerhaavia (2) and Acleisanthes; has described new species of Leptotaenia and Gilia; and has revised the nomenclature of a number of species of Astragalus, including descriptions of 4 new species.—B. FEDTSCHENKO (Acta Hort. Petrop. 19: 183-349. 1902) has published a detailed revision of Hedysarum, recognizing 78 species, of which 3 are new.—J. M. C.

IN THE PRESENT PAPER Neger¹⁴ has extended the ecological studies begun on Phyllactinia to the whole family of the Erysipheae. Very interesting data are given as to the methods of attachment, as also the setting free and distribution of the perithecia, and the scattered observations of a number of authors are brought together and summarized. The perithecia of Sphaerotheca and Erysiphe are not spontaneously set free from the substratum, and the appendages here serve for attachment. On the other hand, the perithecia of Podosphaera, Trichocladia, Microsphaera, and some Uncinulas are broken loose as a result of unequal shrinkage of the upper and under walls of the perithecia in drying. This makes the ripe and dry perithecium either flat or concave on its under side, as has also been observed by Galloway. Just how this deformation leads to the setting free of the perithecia is perhaps still not clear. The interlacing of the appendages serves to hold adjacent perithecia together so that they fall from the host leaf in masses rather than singly. In Phyllactinia the perithecia are set free by the bending downwards of the spine-like appendages which thus lift up the perithecium from the surface of the leaf. The author also discusses the question as to the causes which lead to the formation of the sexual and asexual fruit organs, and concludes that the conidia are favored by a fresh vigorous condition of the host plant, while the perithecia are more likely to be formed in well developed mycelia on mature parts of the host, which, however, must not have been already exhausted by a too abundant crop of conidia.

The earlier paper¹⁵ describes very extensive germination experiments and studies on the form, length, irritability, etc., of the germ tubes of the

¹⁴NEGER, F. W., Beiträge zur Biologie der Erysipheen. Flora 88: 333-370. pls. 16-17. 1901.

¹⁵NEGER, F. W., Zur Kenntniss der Gattung Phyllactinia. Ber. Deutsch. Bot. Gesell. 17: 235. 1899.

conidia. The author believes that in such genera as *Erysiphe* the characters of the germ tubes may be advantageously used in defining the limits of difficult species. In every case the germ tubes showed themselves incapable of nourishing themselves from any nutrient media offered. Their size was limited strictly by the amount of reserve material present in the spore. Different lots of conidia also varied widely in the percentage of germination. Light favors germination and the germ tubes are in many cases positively heliotropic. In many cases also the germ tubes show themselves sensitive to contact stimuli. A considerable series of infection experiments were made, and although the evidence was by no means conclusive many results indicated that in the mildews, as in the rusts, we have numerous cases of physiological species, inhabiting only one host plant, within the limits of the species as at present commonly accepted. Cases are also pointed out in which it seems likely that the ascospores may be capable of infecting a wider series of hosts than can the conidia. The theoretical aspects of the data so obtained are discussed at some length. A further interesting observation of the author is that the little known conidia of *Phyllactinia* are borne in the ordinary basipetal series and not singly as described by Tulasne. Of theoretical interest further is the suggestion that the development of hyphae and haustoria, which penetrate to the interior of the host leaf, as described by Palla and Smith, is correlated with the degree of hypertrophy produced by haustoria in the epidermal cells of the host. The haustoria restrict themselves to the epidermis in cases like *Sphaerotheca*, in which the cells of the latter are hypertrophied, and thus (?) produce an abundant food supply for the parasite.—R. A. HARPER.

RECENT CONTRIBUTIONS TO AMERICAN PHYTOGEOGRAPHY: the Eastern United States.—E. F. WILLIAMS (*Rhodora* 3: 160-165. 1901) makes a comparison of Mounts Washington and Ktaadn, finding general similarity. Mount Ktaadn, however, has a more rugged and arctic aspect, the timber line being exceedingly low; an interesting colony of lowland plants was found well up toward the summit.—J. W. HARSHBERGER (*Plant World* 5: 21-28. 1902) gives a brief ecological account of Mount Ktaadn, in which the lowland timber areas are also described.—C. D. HOWE (*Science* 15: 462. 1902) gives a preliminary account of his studies on a delta plain in Vermont; the development of the vegetation is traced from the beach, through the *Pinus rigida* stage, to the culminating forest of beech and maple. The life history in Vermont is found to be essentially like that in Michigan, as worked out by Cowles and Whitford.—C. H. SHAW (*BOT. GAZ.* 33: 437-450. 1902) discusses very suggestively the development of vegetation in morainal depressions near Woods Hole. Physical agents are found to control the filling of ponds in some cases, as evidenced by open marginal belts of water. *Euthamia graminifolia* flourishes on sandy shores by reason of its running stems; beyond this there are no plants until the depositing zone is passed, where *Limnanthemum* and other runnerless plants occur. Marginal ditches

about floating mats are explained by the great abundance of falling leaves, which smothers out the vegetation. The vegetation is not xerophytic in structure in the earlier stages.—A. HOLLICK (Bull. N. Y. Bot. Gard. 2 : 381-407. 1902; see also *Torreya* 2 : 58-59. 1902), in a paper dealing chiefly with geological phenomena, gives a short account of the vegetation of Cape Cod. Apparently the dunes of Provincetown were once well forested, while it is now difficult to secure artificial reforestation. To account for this Hollick advances the view that a forest can develop *pari passu* with the increasing piles of sand; if, however, the trees are cut off, the drifting sand makes reforestation difficult or impossible. The vegetation is treated in two groups, that of the forest (dominated by *Pinus rigida*, *Quercus rubra*, and *Q. velutina*), and that of the bare sands, subdivided into beach and dunes. Reference has previously been made (BOT. GAZ. 31 : 134. 1901) to the excellent work of HOLLICK on the forests of New Jersey.—J. W. HARSHBERGER (Proc. Acad. Nat. Sci. Philadelphia 1900 : 623-671) has made an ecological study of the New Jersey strand flora. He finds a plantless lower beach, a middle beach with *Cakile* and other succulents, and an upper beach with much *Oenothera humifusa*, a plant of southern range. The seaward dunes are dominated by *Ammophila*, while farther inland *Myrica cerifera* and *Hudsonia* assume the leading place. The tree-clad strand is dominated by weather-beaten junipers, and there is also a jungle zone of trees, shrubs, and lianas. The salt marshes are also considered.—C. F. SAUNDERS (*idem* 544-549) describes the pine barrens and sphagnum bogs of New Jersey.—A. MACELWEE (*idem* 482-490) considers the flora of Edgehill ridge, Montgomery county, Pa., three societies being discussed, namely, sunshine, shade, and sphagnum bog.

T. H. KEARNEY (Contrib. U. S. Nat. Herb. 5 : 261-319. 1900) has published a short but interesting account of the vegetation of Ocracoke island, North Carolina. While many forms are common to northern beaches and dunes, such plants as *Croton maritimus* dominate on the beach, and *Uniola paniculata* on the outer dunes. Live oaks rule in the groves, and *Ilex vomitoria* in the thickets. The salt marshes have many familiar northern types. The mingling of salt and fresh water forms is explained by alternations of salty spray and rainfall; perhaps, however, fresh conditions are encroaching upon the salt, leaving the salt marsh forms as relicts. Interesting anatomical studies upon salt marsh plants confirm the prevalent notion of their xerophytic structure. The island is placed in Merriam's Austroriparian, though many typical plants are absent and others present.—D. S. JOHNSON (BOT. GAZ. 30 : 405-410. 1900) gives some ecological notes on the seed plants and algae at Beaufort, N. C.

T. H. KEARNEY (Contrib. U. S. Nat. Herb. 5 : 321-585. 1901) gives a most excellent account of the vegetation of the Dismal Swamp region. The paper is splendidly illustrated with plates and numerous figures, and is one of the most valuable of recent contributions to plant geography. He regards the region as belonging to Schimper's ever-moist warm temperate zone, though differing

from most similar regions in that deciduous trees dominate instead of evergreens. The salt marshes with *Spartina*, *Salicornia*, and other characteristic plants pass gradually into *Typha* swamps. Among the noteworthy "adaptations" are sheaths which prevent the access of salt water, anchoring rhizomes, and a number of well-known xerophytic structures. The beach flora is sparse, and resembles the more northern beaches. Dunes are well developed and are in some cases eighty feet high; *Ammophila* is the character plant of the outer dunes, but the more southern *Uniola* also has a place. The occurrence of *Salix longifolia*, *Cephalanthus*, and *Baccharis* on the dunes is cited as an evidence of the sand moisture; perhaps they also indicate the advance of a dune over a swamp. The occurrence of *Acer rubrum* and *Nyssa sylvatica* on the lee dune slopes may have a similar explanation, as is the case on Cape Cod. The abundance of *Pinus Taeda* with live oaks on the forested dunes gives a southern aspect, though many of the character plants remain such far to the northward; lianas are highly developed. The usual xerophytic "adaptations" are noted, though neither the soil nor air is dry. The character of the drainage is the chief factor which determines the nature of the inland vegetation. *Pinus Taeda* is the leading forest tree, though it is readily followed by hardwoods in most places if removed. Abandoned fields are first colonized by *Andropogon virginicus*, and later by pines. The leading deciduous tree is Liquidambar, although oaks are abundant; *Fagus* occurs in rich soil. The swamps are of two types: (1) the dark or black gum swamp, which contains *Acer rubrum* and *Taxodium* as well; (2) the light or "Juniper" swamp, in which *Chamaecyparis* rules, and in which there is less water, though what occurs is more acid. This region is the northeastern terminus of Merriam's Austroriparian; many southern and a few northern plants reach here their limits. The analysis of many important topics is keen, and the paper is a highly welcome addition to ecological literature.

C. C. ADAMS (Biol. Bull. 3:115-131. 1902) in a most valuable paper discusses the southeastern United States as a center of distribution. His data are derived in the main from zoological material, but his conclusions are of general interest. Among the criteria for determining a distribution center, aside from fossil evidence, he gives the location of greatest differentiation, of dominance or abundance, of maximum size, of productiveness, of continuity and convergence of lines of dispersal, of least dependence upon a restricted habitat, of continuity and directness of variation along radiating lines of dispersal. Using these and other criteria Adams shows the southeastern United States to be a great center of dispersal, at least for animals. The chief highways have been the Atlantic coast, the Mississippi valley, the Appalachian mountains. He makes a just plea for the dendritic as against the zonal study of life; lines of dispersal and divergence give a clue to many of the great biological problems. This type of study is dynamic and genetic, and thus has a great advantage over the more common methods.—Reference has been previously made to the work of KEARNEY in the Appalachian

region (BOT. GAZ. 31:208. 1901), also to GATTINGER's Tennessee flora (BOT. GAZ. 32:428. 1901), in which the various regions of the state are described as to their vegetation.

R. M. HARPER (Bull. Torr. Bot. Club 27:320-341; 413-436. 1900) has given some interesting data concerning the flora of Georgia. Northern and southern Georgia are quite different, the former having a flora like that farther north, while southern Georgia has true southern types. Lists are given of many plant communities. More recently (Science 16:68-70. 1902) the same author has written a brief account of the botanical features of the Lafayette and Columbia formations. He finds that it is possible to distinguish these formations by the plants which grow upon them. *Eriogonum tomentosum* and *Froelichia Floridana* especially characterize the Columbia sands. Harper (Bull. Torr. Bot. Club 29:383-399. 1902) has also published a paper which deals with the distribution of *Taxodium*. He thinks that there are two species, *T. distichum* and *T. imbricarium*, and that the latter always occur on Lafayette soil, the former never. It seems to the reviewer that *T. imbricarium* will prove to be merely an ecological variety, similar to varieties of ferns and violets which Sadebeck years ago experimentally transformed to the parent species.

C. L. POLLARD (*Plant World* 5:8-10. 1902) notes how the mangroves and other species assist in the formation of the Florida keys, commencing where the corals leave off. *Rhizophora* is the pioneer, but is soon followed by *Laguncularia* and *Conocarpus*. When the mangroves die out, we have the "hammock" land.—CHAS. MOHR's flora of Alabama has been reviewed in these pages (BOT. GAZ. 32:371. 1901). This work is one of the most complete and satisfactory that has yet appeared in this country, being nothing less than a mine of floristic and ecological information. He notes that in Alabama Merriam's life zones correspond with the geological formations rather than with the climate. The hemlock and sweet birch occur far from their main range, and are relicts of the glacial invasion. A number of interesting endemic and local forms are noted.—LLOYD and TRACY (Bull. Torr. Bot. Club 28:61-101. 1901) have made an ecological study of the insular flora of Mississippi and Louisiana. This paper is a noteworthy addition, especially as it gives us a means of comparing our northern and southern coasts. The islands are deposits of Mississippi river detritus; in some cases the mud is still the surface material, in other cases it is covered by sand. On the beach northern forms like *Salsola* and *Strophostyles* are mingled with the more tropical *Ipomoea*. Dunes are formed by *Panicum amarum* and *Uniola*. The palm *Serenoa*, and other plants form "pedestal" dunes. Sand plains are described of various types, culminating in a forest of pines and live oaks with an undergrowth of palms. A unique set of vegetation conditions is found on the shell strand. Among the leading salt marsh plants are *Batis*, *Avicennia*, and *Salicornia*.

A. J. PIETERS (U. S. Fish Commission Bull. 1901: 57-79) contributes an

important paper on the plants of western Lake Erie. The groups of water and swamp plants are presented. The usual hydrophytic "adaptations" are found, and a number of anatomical figures are given. Some excellent plates, showing the life forms of character species, especially *Chara*, accompany the article.—H. W. CLARK (Proc. Ind. Acad. Sci. 1901:128-192. 1902) gives a list of plants with ecological notes from Eagle (or Winona) lake, Indiana, and vicinity.—MISS LUCY YOUSE (*idem* 192-204) discusses the plant ecology of Winona lake. She treats the dynamics of the vegetation, sketching the changes from the lake and swamp stages to the forest or prairie, and from the bare morainic hills to the forest of beech and maple.—W. M. MILLS (Chicago: The Quadrangle Press. 1902) has also studied the above lake, mainly from the standpoint of physiography, but adds some ecological notes.—M. T. COOK (Proc. Ind. Acad. Sci. 1901:266-272. 1902) sketches the development of vegetation in abandoned rock quarries at Greencastle, Indiana.—E. J. HILL (Bull. Torr. Bot. Club 29:564-570. 1902) gives some notes on recent adventures in the Chicago flora.—F. E. McDONALD (Plant World 3:101-103. 1900) describes a sand dune flora in central Illinois, along the Illinois river. Dunes of pure sand, some a hundred feet high, are formed. *Quercus Marylandica* is the leading tree. As might be expected, many species are common to the Lake Michigan dunes.—H. C. COWLES' paper on the physiographic ecology of Chicago and vicinity appeared in this journal (BOT. GAZ. 31:73-108, 145-182. 1901), as well as H. N. WHITFORD'S paper (*idem* 289-325) on the genetic development of the forests of northern Michigan, and E. J. HILL'S paper (*idem* 29:419-436. 1900) on the flora of the White Lake region, Michigan.—C. A. DAVIS (Jour. Geol. 9:491-506. 1901) has confirmed his previous view on the origin of Michigan marl (see BOT. GAZ. 31:361. 1901), and adds some new results.—EMMA J. COLE'S catalogue of the Grand Rapids (Michigan) flora has been noticed (BOT. GAZ. 31:437. 1901); a number of southern trees, such as *Asimina*, *Cercis*, *Carya*, *Morus*, *Nyssa*, *Gymnocladus*, *Liriodendron*, *Cornus florida*, probably find here their northern limit.—V. M. SPALDING (Science 15:402. 1902) has projected a survey of the Huron valley, Michigan. The influence of artificial changes on certain plastic forms has been very great.—H. S. REED (BOT. GAZ. 34:125-139. 1902) has contributed the first paper to the above survey. His topic is the ecology of a glacial lake, and the paper is particularly valuable because of its dynamic treatment and careful quantitative work.—H. C. COWLES' paper dealing with the influence of underlying rock upon the vegetation has been reviewed previously (BOT. GAZ. 33:316. 1902)—B. E. LIVINGSTON (Report Mich. Geol. Surv. 1901:79-103. 1902) has published on the distribution of the plant societies in Kent co., Michigan. His results will soon be published in this journal, and it may be merely noted here that his physiographic results agree with those of the reviewer. He strongly urges the moisture-retaining power of the soil as the decisive factor in plant distribution.—E. BRUNCKEN'S valuable studies in Wisconsin have been noted (BOT. GAZ. 34:149. 1902).—H. C. COWLES.

NEWS.

DR. THEODOR VON HELDREICH, director of the Botanical Gardens at Athens, died recently at the age of eighty years.

PROFESSOR A. ENGLER, of the University of Berlin, has been for some time engaged in a botanical expedition to Africa.

PROFESSOR F. E. WEISS, of Owens College, Manchester, England, has been visiting some of the prominent botanical laboratories of the United States.

IN THE NEW EDITION of his *Plant Breeding*, which will probably be in the market next month, Professor Bailey will include a full presentation of the recent theories of De Vries and Mendel.

DR. E. PERCEVAL WRIGHT, Professor of Botany at Dublin University, calls attention to the fact that the Herbarium of Trinity College contains such collections as Harvey's extensive series of Algae, Thomas Coulter's collection of Californian plants, etc., and has kindly offered to give any information in his power concerning them.

ERRATUM.—In Mr. Chandler's paper on *Nemophila* (BOT. GAZ. 34 : 194-215. pls. 2-5. 1902), the legends of *Plates IV* and *V* should be interchanged, *Plate IV* being *N. exilis* Eastwood, and *Plate V* being *N. parviflora* Dougl. As a consequence, the two plate numbers should be interchanged in the "Explanation of plates," p. 215.

ACCORDING to a recent estimate made by the Bureau of Forestry into the losses from forest fires, the conclusion is reached that in an average year 60 human lives are lost, \$25,000,000 worth of real property is destroyed, 10,274,089 acres of timber land are burned over, and young forest growth worth at the lowest estimate \$75,000,000 is killed.

SARGENT'S SILVA OF NORTH AMERICA is complete with the publication of volumes XIII and XIV this autumn. This great work has been twelve years in preparation, contains 750 plates from drawings by C. E. Faxon, and describes and illustrates 567 species of American trees north of Mexico. A new work only less extensive, by the same author and artist, and entitled *Trees and Shrubs*, will begin to appear this autumn. It will be published in several large quarto volumes, with four parts to a volume, and will illustrate new or little known woody plants, especially those of the northern hemisphere which may be expected to flourish in the gardens of the United States and Europe.

BOTANICAL GAZETTE

DECEMBER, 1902

A MORPHOLOGICAL STUDY OF CERTAIN
ASCLEPIADACEAE.CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.
XLI.

THEODORE C. FRYE.

(WITH PLATES XIII-XV)

In a previous paper (7) the results of a study of the pollen of certain Asclepiadaceae were published, and during that investigation the remarkable structure of some of the floral organs attracted attention. The present paper is the result of their study.

The species studied were *Asclepias Cornuti* Dec., *A. Sullivantii* Engelm., *A. rubra* L., *A. phytolaccoides* Pursh, *A. tuberosa* L., *A. incarnata* L., *A. obtusifolia* Michx., *A. verticillata* L., *Acerates longifolia* Ell., and *A. viridiflora* Eaton. The material was all collected in the vicinity of Chicago, and in the field plunged into weak chromo-acetic acid. The safranin, gentian-violet, orange combination proved to be the best stain for critical work, although it was often better to omit the orange. The stages were most completely followed in *A. Cornuti*, and the following account applies to it unless otherwise stated. The chief difficulty lies in the small size of the embryo sac. *A. Sullivantii* is a better form, since it has a larger flower, but it was not found in time for young stages. The other species were examined for comparison, and show essential similarity; but any important disagreement is noted.

The family has received considerable attention, but aside

from taxonomy most of it has centered about the latex and the pollinia. Chauveaud is the only recent writer who has examined the embryo sac. The latex will not be considered in this paper, except incidentally; and pertinent literature will be noted under the different topics. Schacht (10) states that in *A. Cornuti* the primordia of each set of floral members arise simultaneously and separately, while the sets arise in centripetal succession. Chauveaud (3) reports the centripetal order in *Cynanchum* L. (*Vincetoxicum* Moench). Payer¹ is referred to in this connection, but his book was not accessible.

From the upper surface of the somewhat swollen mass of meristematic tissue destined to bear the flowers of the umbel many hemispherical projections arise, each of which gives rise to a single flower. The outer ones are the first formed. This agrees with the centripetal order of opening of the buds in the umbel. Each flower grows from the axis of a bract which slightly precedes it in origin. One might expect that a careful investigation of an hypogynous, apocarpous, actinomorphic, almost polypetalous flower would reveal its acyclic ancestry, but in no case could any precedence be noted among members of the same set, nor any confluence of primordia. The umbels in *A. tuberosa* are terminal, as shown by longitudinal sections through the stem tip (fig. 1), and the same is probably true of the other species.

About the time the carpels appear, the calyx begins a growth of epidermal hairs (fig. 2), mostly on the dorsal surface. Later, when the sepals are reflexed, hairs are also formed on their ventral surfaces, which are then exposed. The sepals are reflexed with the petals at the time of the opening of the bud, but after the latter drop off, the former fold tightly up against the carpels. In this second closing their function is again probably protective. The reflexion of the sepals and petals seems to be due to turgescence of cells on their adaxial sides near the base. It is suggested that perhaps the exposure of the adaxial surface of the basal part of the sepals, due to the dropping off of the corolla, causes loss of turgescence and consequent infolding.

¹Traité d'organogénie comparée de la fleur. Paris. 1857.

The glands do not seem to have been observed by Schacht (10), although they are easily seen with a hand lens. Chauveaud (3) saw them within the calyx of *Cynanchum*, and gives their structure and formation without attempting to explain their function or stating their number. Schumann (11) in characterizing the genus *Asclepias* says the glands within the calyx are paired or single, but makes no mention of their occurrence elsewhere on the plant.

In all the species studied, between the calyx and corolla and alternating with the members of the former, groups of glands were found. In the mature flower there are from one to six in each group, the number and size varying even in the same flower. Usually they are side by side (*fig. 5*), but sometimes they are radially placed (*fig. 6*). They are also scattered singly on the swollen top of the common peduncle. Near the base of a bract of the involucre on its adaxial surface as many as a dozen may be found (*fig. 7*). Dr. H. C. Cowles called my attention to their presence in *A. Sullivantii*, in the axils of the leaves, and and also near the base of the lamina on the adaxial surface of the midrib. I have observed them at the latter point in herbarium specimens of *Asclepias speciosa*, *A. exaltata*, *A. Sullivantii*, *A. Cornuti*, *A. jaliscana*, *A. arenaria*, and would not be surprised if careful examination revealed them in many others.

Taking the development of the glands inside the sepals as an illustration, they appear about the time the carpels begin to show, but on other parts of the plant they appear earlier. At first there is only one representing each group, and it arises from the sepal on its adaxial surface quite near the base and lateral edge. Later others appear on each side of the first and thus the group is formed. The middle (oldest) ones usually remain the largest. In their formation (*figs. 3, 4*) the division of the hypodermal cells forms a protuberance of isodiametric cells over which the epidermis continues. The elongation of the interior cells then increases the length of the protuberance, while the epidermal cells elongate radially over the whole or a part of the surface and function as gland cells, as is shown by their deep stain, volume of protoplasm, and large nuclei (*fig. 8*). These

glands are almond-shaped, the flattening being due probably to pressure, since those on the end of the common peduncle are cylindrical. The base is more or less narrowed into a stalk; and those in the axils of the bracts are two or three times as long, proportionally narrower, and more distinctly stalked. Sometimes the epidermis at the tip is not glandular. Some of those on the end of the common peduncle are as much as 1100μ long including the stalk. They remind one here of multicellular glandular hairs. The evidence as to the function of these glands is negative. Their distribution and early appearance precludes the idea of any connection with cross pollination. I have never seen an insect pay any attention to them, although I have often watched for it.

Chauveaud (3) reports that in *Cynanchum* the corolla, after some elongation, unites with the stamens, but later becomes free. The petals of the species studied are not at any time united with the stamens, although a transverse cut through a bud at an early stage gives such an appearance, because the organs are closely appressed and cut at an angle. At base the corolla forms a short tube, which has probably arisen as a ring from the receptacle. The dorsal surface bears stomata and becomes hairy; and the ventral surface just before the bud opens becomes papillose.

The stamens have been much studied. Schacht (10) gives a figure showing the beginning of hood and horn in *A. Cornuti*. Corry (4) traces the development of the wings in the same species. He also follows the development of the sporangium, wrongly deriving it from a single sporogenous cell. Chauveaud (3) traces the development of the stamen of *Cynanchum* with its hood or horn, and describes some features in the development of the pollen. Strasburger (14), Gager (8), and the writer (7) have given the history of the microspores. Stephens (13), however, seems to have seen the tetrad divisions; and from an unpublished paper now in my hands it seems that Miss Langley, now deceased, of the University of Michigan, traced correctly the pollen formation in 1897.

The stamens and petals early arise from a common ring slightly elevated above the insertion of the other sets. From

the reflexion of the epidermis where the two whorls unite, and from the meristematic character of the cells composing the ring, one is led to conclude that it is of toral origin. The whole stamen in its older stages shows a remarkable tendency to form intercellular spaces, the tissue resembling the spongy parenchyma of a leaf.

The filaments unite to form a ring about the carpels. By their growth upwards against the head the anthers are pushed into a lateral position (*figs. 9-11*). At five points, corresponding to the five lines along which the filaments have united, they do not fit up against the head so tightly. These are the gateways to the stigma.

At the base of the united stamens are two spaces somewhat tetrahedral in form, bounded by the staminal ring and the two carpels. The general tendency towards the formation of loose tissue expresses itself here in the formation of two protuberances from the base of the staminal ring, filling these spaces (*figs. 20, 21*). They are large enough to be seen easily with the naked eye and might be taken for rudimentary carpels, but their late appearance and the bulging of the staminal tissue into them reveals their origin. Eichler (6) figures diagrammatically what he calls disk glands in a similar situation in *Vinca minor*. But these projections in *Asclepias*, while easily mistaken for glands under a hand lens, do not give the dense stain obtained in other glandular tissue of the flower.

Just before the ovules appear, when the pollen has reached the mother-cell stage, the filament pushes out on its dorsal side a crescentic protuberance whose convex side is towards the base, and in whose concavity a papilla appears (*fig. 16*). The crescentic projection is destined to become the hood, and the papilla the horn. The young hood and horn are meristematic at the tip. Spiral vessels appear in the one bundle of each stamen about the time the hood begins to grow. These bend, forming a loop in the hood as it grows larger. When the latter has reached its full development, the vessels extend seven-eighths of the distance to the tip and bend sharply back upon themselves (*fig. 18*). The vessels in the filament must have increased

their length, after thickenings had been formed, to at least fifteen times. Whether this was due to the formation of new cells or to the elongation of those present was not determined with certainty, but I am strongly inclined to believe that both things occur. One finds scattered short cells with very close spirals not yet well marked, beside them may be long cells with spirals so long drawn out that their spiral nature is almost lost, the cell walls perhaps even disappearing, the whole showing disorganization. In fact, all the stages in the ontogeny of a vessel may be found in a single longitudinal section of a forming loop. This makes it appear that the spirals form while the cells are not very greatly elongated; that the elongation of the cell takes place by the widening of the part of the wall between the spirals, due either to growth of the cell or to tension arising from the growth of the surrounding tissues; that when the cell has become extremely elongated it collapses and disorganizes, while several cells beside it have meanwhile formed spirals, thus preserving the vascular continuity. Since there is only one bundle in a stamen, the nutrient solutes would find it necessary to pass to the anthers by way of the tips of the hoods. There is no direct connection between anther and pedicel. The tissue of the inner side of the filament forms aerenchyma, thus being able to keep pace with the curving of the bundle without leaving any great hollow. The mature hood is then largely composed of a tissue resembling the spongy tissue of a leaf, but without chlorophyll (*fig. 19*).

The horn is carried up some distance by the growth of the hood, but has no connection whatever with the fibrovascular bundle (*fig. 18*), as one is led to think from one of Schacht's figures. It seems to be built by the division of the cells near its apex, and the later transformation of its tissue into aerenchyma, for its whole interior is filled with very loose tissue (*fig. 19*). In *Acerates*, as the name implies, there is no horn. However, the bundle passes into the hood as in *Asclepias*, while in *Cynanchum* (3) it simply curves into the base of it. The direction of the bundle in relation to the hood may prove to be of value in determining relations among the *Asclepiadaceae*.

The hood and horn are known to enclose the nectar, but the part played by the horn in pollination is not clear.

The formation of the anthers, with their wing-like projections and two sporangia, as well as the development of the microspores, has been worked out by the writers referred to above. In general, the account is the same for all the species examined.

The development of the male gametophyte is pretty well known. Corry (5) saw the generative and tube nuclei in *A. Cornuti*, but supposed the larger to be the generative cell. Strasburger (14) found the small one to be the generative cell, and the writer (7) found the same in *A. tuberosa*. Gager (8) observed the first division of the microspore in *A. Cornuti*, and the division of the generative nucleus.

A. verticillata proved to be the best form for the study of the pollen grain, and hence it is here taken as the type, although the others agree with it in general features. The generative cell, flattened out against the wall usually in lenticular or hemispherical form (*fig. 22*) and varying in size, soon loosens and approaches the tube nucleus (*fig. 23*). The two nuclei are greatly different in size and both have the chromatin in granular threads. The generative nucleus usually has massed about it a quantity of denser cytoplasm of finer structure and bounded by a definite wall. The wall sometimes persists until division is complete (*fig. 26*), and at other times division follows its resorption (*figs. 24, 25*). The lenticular form is gradually changed to crescentic, oval, or even spherical. The division forming two male cells occurs about the time the buds open. It is not quite simultaneous in the same anther, although the amount of variation is not great. In all cases observed, division occurs near the tube nucleus. In *fig. 25* eight chromosomes were counted, but not with absolute certainty. Those in the vegetative cells of the stamens are about the same in number, contrary to expectation, but they are so extremely small that a definite statement is not warranted. The condition of the cytoplasm in the pollen grains of the same anther seems to vary. In some it is reticulated, in others homogeneous. In almost all one finds groups of the deeply staining bodies of undetermined nature (*fig. 24*). In

A. verticillata they are almost spherical. The determination of their nature has been left to Mr. Gager, who announces work in progress on them. I have found bodies in *A. tuberosa* in the latex tubes resembling those in the pollen of that species in staining properties and in form, thus adding weight to the food theory. In some pollen grains there are single spherical bodies of varying size, resembling those in the groups in their staining capacity (*fig. 25*).

Concerning the pistil Schacht (**10**) states that the two carpels roll in adaxially, each forming a loculus, while the fusion of their tips results in the head (Corry's "style table"). He also figures an ovule showing a nucellus. Corry (**5**) has gone at length into the formation of the head and especially into the origin of the corpusculum and caudicules. Schumann, however, doubts his conclusions. In regard to the development of the ovules almost nothing has been done except in *Cynanchum*, in which Chauveaud (**3**) reports that there is no nucellus, no integument, and only one megaspore.

The arrangement of the carpels in relation to the outermost sepal seems not to be a constant one, although usually one is opposite. The carpels remain separate except at their tips. The loculus formed by the rolling in of the edges opens in the head a short distance above the stigma. The cleft on the inner surface is never completely lost.

Quite early, before ovules appear, before even the edges of the carpels have rolled in to any considerable extent, the tips of the carpels come in contact and begin fusion, forming the head. This is about the time of the first division of the archesporium in the anthers. The ends of the carpels enlarge enormously, forming a somewhat spherical mass (the head) with a funnel-shaped depression at the top, which is sometimes deep, sometimes shallow (*fig. 28*). The fibrovascular bundles of the carpels flatten out, and by the juxtaposition of their edges form a hollow cylinder in the center. At the apex the cylinder spreads, forming a funnel. Corry (**5**) figures it doubling back towards the base, but diligent search revealed no such case. The stigma has long been known to be situated just beneath the head, although some

writers have considered the head stigmatic. Corry (5), limiting the term stigma to that portion fitted for the reception of the pollen, naturally regards the head stylar. One is led to conclude from his statements that he believed the tips of the carpels were abaxially reflexed to the functional stigma, seeing an argument for it in cases of the reflexion of the fibrovascular bundle. The conductive tissue, however, does not follow the path which a definite location in a recurved leaf would give it; and if it is not definitely placed in the carpel, its outcrop, the stigma, is not more definitely located. Those who believed the head to be of stigmatic origin thought the functional stigma to be under the corpusculum. The question here is a phylogenetic one. Has the stigma always been where it now is, the head developing above it later; or, teleologically speaking, has the stigma moved to adapt itself to the modifications of the floral organs? The papillose epidermis of the funnel-shaped depression in the top of the head, the suggestion of conductive tissue in appearance of the cells beneath this epidermis, the absence of a downward curve in the tips of the bundles, and the continuation of the conductive tissue above the functional stigma, all indicate that the homologue of the stigma in other plants is the funnel. We may then regard the head as an abaxial thickening of the style immediately beneath the stigma. We would then have later the formation of a new stigma beneath the head, and the cessation of functional activity in the one at the top. The strongest argument in favor of Corry's theory, however, and one not mentioned by him, is found in the Apocynaceae. Here one finds stigmas on the equator of a fusiform head, a stage between the terminal stigma of the Gentianaceae and the subcapital one of the Asclepiadaceae.

Incidentally, many of the stages in the formation of the caudicules and corpuscula were observed and Corry's account (5) confirmed.

The conductive tissue lines the placenta and the canal that forms the continuation upwards of the cavity of the ovary. Just beneath the head it spreads out as a disk or funnel, reaching the surface in a circle under the head (*fig. 28*). The stigma there-

fore forms a band completely surrounding the head at that level, but because the upward projections of the styles unite closely with the head, the stigma is accessible only through the alar chambers, corresponding to the intervals between the stamens. The conductive tissue lines the canal to its end.

In the formation of the ovules rounded projections (*fig. 29*) are pushed out in longitudinal rows, the lowest in each row being the oldest. Before there is a distinct differentiation of funiculus, one of the hypodermal cells at the upper outer angle of the ovule can be recognized by its larger nucleus and different stain as an archesporial cell (*fig. 29*). Occasionally one finds two or three archesporial cells side by side (*fig. 30*), but in such cases one seems to outgrow the others, for in no case was more than one in its later well developed stage (*fig. 31*) found in the same ovule. The epidermal layer over the archesporial cell is the only sterile part of the nucellus. Schacht (*10*) figures a nucellus projecting from the ovule like a papilla. Such forms I could not find in *A. Cornuti*, and they must be exceptional. By the cessation of growth in the nucellus, and its continuation around it to form the single integument, the nucellus comes to appear deeply sunken (*fig. 34*). The nucellus is short lived, being very soon replaced by the embryo sac. It seems remarkable that there should be no nucellus or integument in *Cynanchum* as reported by Chauveaud. If one takes the view that he overlooked an evanescent nucellus his story accords well with that in *Asclepias* and *Acerates*, his "revêtement protecteur très épais" becoming the integument. Its appearance and manner of formation are about the same as the integument of the genera studied.

The archesporial cell reaches a size equal in section to a dozen of the surrounding cells. No parietal (tapetal) cell is cut off, and by two successive divisions a row of four megaspores is formed (*figs. 32, 33*). This does not always occur during the same stage in the development of the integument, as sometimes it occurs when the nucellus is not yet covered, and at other times when the nucellus is deeply imbedded in the body of the ovule. To avoid confusion the two cells resulting from the first division of the archesporial cell will be called daughter cells.

Both daughter cells and megaspore will be numbered beginning nearest the micropyle.

The number of chromosomes in the division of the archesporial cell could not be determined. In the division of the daughter cells of *A. Sullivantii* five were counted in several cases, but not with certainty. There are approximately half as many, however, as in the vegetative cells. The two daughter cells do not always divide simultaneously. In *A. tuberosa* only one case of this division was observed, and in that they were not widely separated in time, although the micropylar daughter cell was the later to divide, and the spindle in it (fig. 33) was smaller. In *A. Sullivantii* many dividing daughter cells were found, and in no case were the divisions in the same ovule simultaneous. In some cases, however, the equality of the megaspores leads one to think that this may sometimes be the case. In the cases observed, the second daughter cell was always the first to divide (figs. 39, 40). The difference in time appears to vary, if one may judge from the difference in development of the third and fourth megaspores at the time of division of the first daughter cell. Sometimes the third and fourth megaspores have undergone little change when the first daughter cell divides; sometimes one of the two has considerably enlarged, usually the fourth; and sometimes the third is already largely resorbed (fig. 39). The fourth megaspore does not always function as the embryo sac, but any one of the four may, the relative frequency rapidly decreasing from the fourth to the first. All were seen to form sacs in *A. Sullivantii* except the first (fig. 41), and very probably that could be found. The first was seen to form the sac in *A. tuberosa* (fig. 36). Occasionally one finds two megaspores growing alike (fig. 37), but that one is finally crowded out is evident from the absence of more than one mature embryo sac in an ovule. The functioning of other than the most deeply seated megaspore has been reported before in several cases, but its frequency in *A. Sullivantii* is rather remarkable. In perhaps 10 per cent. of the cases observed the fourth megaspore did not become the embryo sac. In *A. tuberosa* and *A. Cornuti* the per cent. is much smaller.

The resorption of the three arrested megaspores takes place rapidly, so that one might easily overlook the stage completely. In *A. tuberosa* the megaspores farthest from the functioning one seems to be resorbed first (figs. 35, 36). One would suppose that the nearest would be the first to disappear, for in the disorganization of the surrounding cells those nearest are the first to change. In *A. Sullivantii*, from the cases of disorganization of the third cell while the first and second are still in good condition, one gets the suggestion that before the first daughter cell divides it offers greater resistance to disorganization than it does later. From fig. 40 one is led to conclude that the first daughter cell before its division either aids in the disintegration of the third megaspore or utilizes its space as the fourth absorbs it.

Among the Asclepiadaceae, therefore, we find one of the strongest arguments for homologizing the row of four cells in the ovule with the tetrad of microspores. It is known (7) that in the formation of microspores each cell of a hypodermal archesporial plate divides, forming a parietal and a primary sporogenous cell. The latter without division functions as a mother cell, which gives rise, with reduction of chromosomes, to a row of four microspores, each of which develops a male gametophyte. In the formation of megaspores usually a single hypodermal archesporial cell does not divide to form a parietal cell, but functions directly as a spore mother cell, giving rise, with reduction of chromosomes, to a row of four megaspores, any one of which may develop a female gametophyte.

But what is the significance of the retardation in the division of the first daughter cell? No cases of the first preceding the second are reported, and the question as to the origin of this retardation becomes pertinent. In tetrad formation among the pteridophytes the daughter cells divide simultaneously. The possibility of a relation between the retarded division and the suppression of functional activity in three of the four megaspores is suggested. If such a relation exists, there are three possibilities:

1. The suppression of three of the four megaspores may cause the retardation in division of the cell forming two func-

tionless ones. This would presuppose some unknown cause operating to suppress three, probably the same which operates to reduce the number of megaspores in heterosporous pteridophytes. It has been suggested that the central position of the fourth megaspore gives it an advantage over its fellows in food supply. If nutrition is obtained from the resorption of the surrounding cells and the influx of food stuffs, this claim receives added weight when it is remembered that the fourth megaspore is nearest the point where the later formed vessels end. The retardation would then be regarded as the beginning of the suppression of a useless division. The apparent variation in the relative time of division of the two daughter cells adds weight to this view, and cases like *figs. 38* and *39* suggest that there may be here a transition between the row of four and of three. If one were to find a case like *fig. 38* alone, it might easily be mistaken for an example of the formation of only three megaspores; but from the size and appearance of the nucleus of the first daughter cell, and from the fact that such stages must have been passed by *fig. 39*, it seems clear that the first daughter cell would have divided again. But if retardation were more pronounced in a case like *fig. 39*, one can readily see that resorption might occur before the first daughter cell divides, and the condition of three megaspores would be established. It is possible that in some such way the reduction in numbers of megaspores took place in those spermatophytes in which only three or fewer megaspores have been reported.

2. The retardation in the division of a daughter cell may cause suppression of some megaspores. This would presuppose some unknown cause for the retardation. The earlier division of the second daughter cell would no doubt give the third and fourth megaspores an advantage over the first and second, but it would not account for the much more frequent predominance of the fourth than of the third unless the relation to food supply were again introduced.

3. Both retardation and suppression may be due to a common unknown cause.

That retardation in division resulted from loss of function

seems to be the most satisfactory hypothesis at present. Since no case of retardation in division of the second daughter cell was observed, it would be interesting to know the relative time of division of the two when the first or second megaspore predominates. Since only one case of the division of the daughter cells was observed in *A. tuberosa*, no conclusions can be drawn concerning the meaning of the smaller spindle in the first.

The embryo sac passes rapidly through the typical two, four, and eight-nucleate stages (*figs. 42, 43*), and the usual ante-fertilization stage of the sac is reached. Occasionally one finds more than three antipodals (*fig. 45*), but it is quite the exception, and only once were fewer than three noted. The synergids resemble the egg very closely in many cases and can be distinguished from it only by the relative nearness of their nuclei to the micropyle (*figs. 43-46*). The number of cells at the micropylar end was constant, although Chauveaud (3) figures five micropylar cells in the sac of *Cynanchum*, and believed that the five embryos sometimes found were due to the fertilization of all of them. The sac enlarges very rapidly, soon destroying the nucellus and much of the surrounding tissue. In one case noted it had replaced the surface of the ovule (*fig. 44*), while in several instances it had come near it.

In this connection it may be noted that in two ovules a tracheid was observed near the base of the embryo sac and slightly projecting into it, showing that the thickening of their walls had occurred before the sac had reached its full development (*fig. 48*). In only two other genera of angiosperms has the occurrence of tracheids in the nucellus been reported: in *Castanea* by Miss Benson (1), and in *Casuarina* by Treub (15). The occurrence of a tracheid near to such a rapidly enlarging embryo sac raises the question whether increased conduction had not been the cause of its formation. That increased conduction leads to increased formation of tracheary tissue seems evident from Vöchting's experiments with the potato and other tubers. That it causes the formation of tracheary tissue where there has been none phylogenetically there is no evidence except in the evolution of vascular from non-vascular plants. Could the tracheids

radiating from the base of the ligule in *Isoetes* (12) have any relation to those in the ovules of *Asclepias*? In any event, in the ovule one would expect the formation of leptome rather than of hadrome from such a cause. This throws us back upon Miss Benson's (1) suggestion that this is an indication of a degenerate chalazal vascular strand once extending into the nucellus. Judging from the form and arrangement of the cells between the end of the vascular bundle, which appears later, and the sac, the tracheid is just about where the former, extended, would meet the latter. That a primitive feature so nearly lost, even among the lower *Archichlamydeae*, should appear among the *Asclepiadaceae* seems remarkable, and suggests a doubt as to its primitive character.

The fertilization of the *Asclepiadaceae* has long been a subject of interest. According to Corry (5), Robert Brown saw the pollen tubes in the ovary and noticed that they were attached to the ovules, but like all other botanists of his time he supposed the tubes reached the ovary by way of the caudicules and the head. According to Brongniart (2), Ehrenberg rediscovered the tubes, but considered them permanent structures. He observed that the tubes issue from the side of the pollinium, thus disproving the theory of fertilization through the caudicules, and leaving the location of the stigma in doubt. Two years later Brongniart (2) properly located the stigma, and traced pollen tubes from the pollinia into the style. Since he wrote before insect pollination had received much attention, he accounts for the development of the pollen tubes within the anther by the passage of a hypothetical liquid from the corpusculum into the pollinia by way of the caudicules. Whether pollen tubes do sometimes form within the anthers, or whether Brongniart was mistaken in the location of the bursting pollinia is still a matter of doubt. Corry (5) says that flowers artificially pollinated with their own pollen remain sterile, although the tubes penetrate the style. He observed one nucleus, probably the tube nucleus, enter the tube, and traced the tubes to the ovary. Chauveaud (3) reports that in *Cynanchum* he found pollen grains putting out tubes within the anther. Gager (8) reports that in *A. Cornuti* the tube nucleus

enters the pollen tube in advance of the male cells. He found the tubes in the micropyle, and the two male cells, when they reached the ovule, were still spherical and unaccompanied by the tube nucleus.

The pollen tubes penetrate the stigma in a mass and pass down the hollow of the style. All penetrate into the same ovary. The tissue seems to be no obstacle; for they could get into the stylar canal without such penetration by a slightly less direct route. In the ovary they spread out, fan-like, over the surface, forming a mat. To reach the micropyle a tube grows up between the ovules, or when the ovules are somewhat isolated it follows the funiculus, or even passes directly across the cavity to reach its destination. Reaching the sac it usually passes along the inner surface of the wall until it gets above the synergids, where it seems to burst, discharging the contents for some distance into the sac. Sometimes one of the synergids is destroyed, but there seems to be no regularity about it. In *A. tuberosa* the male cells are in advance of the tube nucleus and near the tip of the tube when it penetrates the stigma (*fig. 47*), differing in this respect, according to Gager, from *A. Cornuti*. In their passage down the tube the male cells advance more rapidly than the tube nucleus, so that the latter reaches the upper part of the ovary about the time the male cells enter the embryo sac. The tube nucleus goes no further, and may be found there after the endosperm has begun to form. Experiments with tubes grown in weak sugar solutions show, as one might expect from their delicacy, that the tubes are very sensitive to changes in osmotic pressure. By slight changes one can cause the contents to flow back and forth in the tubes without injuring the walls. The flow can be watched under a compound microscope. When the tubes are burst by too rapidly decreasing the osmotic pressure on the outside the rupture is always at the tip. This raises the question whether in killed material much dependence can be placed upon the position of the nuclei in the tube, either in reference to one another or to the end of the tube. The killing fluid might easily cause flowing and change in position, and the sensitiveness of the delicate tubes to changes in osmotic pressure makes it seem

probable that this often occurs. It seems that the normal bursting of the end of the tube after penetrating the embryo sac might be due to the same cause.

The polar nuclei have usually not fused when the tube bursts. The antipodal one is somewhat below the middle of the sac, while the micropylar one is usually somewhat above it (*fig. 48*). Before the polars have fused, one of the male cells unites with the antipodal one, and about the same time the other male cell fuses with the egg (*fig. 48*). The male cells are crescentic in form, reticulated with granules, and not conspicuously unlike in size. In one case a male cell was found fusing with the polars after their union. This does not seem singular, however, when we recall the method of pollination. Insect pollination requires some range in time for the process. Fertilization may then occur at different stages, or the embryo sacs must remain stationary in the proper stage until the male cells arrive. But unfertilized ovaries show that the embryo sacs pass into the seven-celled stage (*figs. 43, 44, 46*); that is, the polars unite whether fertilization has taken place or not. Again, the older ovules are nearer the base of the ovarian cavity, while the pollen tubes enter in a mass at the top. The younger ones it seems, in any given ovary, would be fertilized first, with the result that fertilization in different stages of fusion of polars would occur. In fact, the literature of double-fertilization gives us instances of fertilization before, during, and after fusion of polars, but not all in the same species. The fusion of a male cell with the antipodal polar is characteristic of *A. Cornuti* when fertilization occurs before fusion of the polars; but it is not unique in plants, for Guignard (9) reports seeing a case of it in *Lilium Martagon*. He thinks, however, that the male cell goes to the polar nearest it at the time of its issue from the tube. The conditions in *A. Cornuti* make such a theory improbable, at least for that species. The micropylar polar was in all the cases observed nearer the end of the tube than the antipodal (*fig. 48*), yet in all cases of fertilization before polar fusion the male cell fused with the antipodal polar. If the male cells have independent motion, the question arises as to what impels the male cell in one plant to seek the

micropylar polar and in another the antipodal. To say that the upper polar has the greater attraction because it is sister to the egg is not sufficient, for in *A. Cornuti* the polar most distantly related to the egg has the greater attraction. Nor will proximity account for it, for the micropylar polar is nearer the end of the tube than the antipodal. It might be supposed that incidentally this lends weight to Strasburger's view that the male cell is carried by the streaming of the protoplasm, but in this case we should have to suppose the streaming to be towards the antipodal polar. If the polars are in any way carried by the stream, we should expect that the streaming would more often be from the end of the tube towards the farthest polar, but that the polars are carried to any considerable extent is doubtful. Another objection is the proximity of the micropylar polar in some cases to the end of the tube. It seems as though the male cell would unite with the micropylar polar if the latter had the same affinity for it as the antipodal polar. On the whole, I am inclined to believe that the antipodal polar has for some unknown reason a stronger attraction for the male cell than has the micropylar.

The sac after fertilization is greatly increased in size by the development of the endosperm. The first division of the endosperm nucleus occurs soon after fertilization, but the actual division was not observed. The second and third divisions rapidly follow, forming eight endosperm nuclei (*fig. 50*). Up to this time the nuclei divide simultaneously and no walls are formed. The number of chromosomes in the endosperm could not be determined, but there were more than in the megasporos. In many cases there was a tendency towards the massing of the endosperm about the egg. The cytoplasm of the sac seems to increase in volume as the number of free nuclei increases. In the eight-nucleate stage of the endosperm the formation of the walls by indentation begins (*fig. 50*). The division into sixteen nuclei seems to be nearly simultaneous, since few cases could be found where there were between eight and sixteen nuclei. By this time the cells have become somewhat walled off (*fig. 51*), and the divisions from this time on are not simultaneous. The

antipodals may still be seen flattened out against the sac-walls when there are approximately thirty-two endosperm nuclei (*fig. 52*). Frequently in this stage one of the synergids could still be recognized as a small, poorly staining nucleus, crowded into the space at the base of the egg (*fig. 52*).

The egg after fertilization forms a distinct wall and rests. No division occurs before the endosperm has passed its sixteen-celled stage (*fig. 51*). This leads one to question whether the reported cases of endosperm division before fertilization, *e. g.*, *Casuarina* (15), may not be due to misinterpretation, the resting egg being mistaken for an unfertilized one.

Some changes of interest occur in the ovule after fertilization. Before fertilization the placenta begins the formation of a longitudinal ridge under each row of funiculi. This continues to grow higher until when the seeds mature it is a membrane about 3^{mm} high. In it can be seen plainly with the naked eye the bundles passing to the ovules. On account of the growth of the lateral portions and ends of the ovules, and possibly pressure from the ovary wall, funiculo-micropylar flattening takes place. It seems that growth along the sides has most to do with the flattening, for the tissue in the edges is quite meristematic. About the time of the third division of the endosperm the epidermis at the micropylar end of the ovule—the one nearest the top of the ovary—becomes intensely active. The cells elongate enormously and form the pappus. The hairs composing it remain single cells with a single nucleus in each. Chauveaud (3) reports two nuclei in each in *Cynanchum*. The pappus is tightly packed in the grooves between the placental ridges, and the free ends extend towards the apex of the pod. The micropyle in *A. Cornuti* and *A. Sullivantii* is still visible with a hand lens when the seed begins to turn brown. The funiculus never thickens much, so that in its later stages it is little more than a vascular bundle and is very easily broken off.

The changes resulting in the formation of the pod also deserve attention. At or shortly before the time of fertilization, the outer epidermis becomes active, as is shown by its deep stain and protoplasmic contents. The surface usually becomes

covered with papillae, specially where the ovary narrows into the style. The papillae in *A. Cornuti* sometimes develop into long finger-like projections, as observed by Brongniart (2), although sometimes they form only rounded knobs. Fertilization causes the rapid development of a dense covering of hairs on the outer surface and sometimes a few on the inner. Each hair is composed of a single row of cells which arises from an epidermal cell. Another result of fertilization is the development of a meristem layer just beneath the inner epidermis. There are signs of this meristem just before fertilization, but it remains only a sign unless fertilization occurs. The result of the activity of this meristem is the rapid thickening of the ovary wall, which is accompanied by the formation of dorsiventral bundles. Preceding fertilization there is in the carpel only one bundle, centrally located. From this other bundles form laterally when pod formation begins, but at first all are parallel to the surface of the carpel. The elongated elements which later form the dorsiventral vessels were first noticed when the endosperm was in the two to eight-nucleate stage. With the formation of dorsiventral vessels there is a rupture of the parenchyma between them, forming cavities. These are well under way by the time the egg undergoes its first division. Further development of the cavities results in the formation of a pod composed of two walls separated by a large space bridged only by bundles with a casing of parenchyma. The cavities extend even into the papillae, which in the mature pod vary from almost nothing to 6^{mm} in length. The dorsal bundles remain closely applied to the dorsal wall of the cavity. The layers of cells next the inner surface become elongated in different directions, forming a firm layer which shows a smooth surface on the side next to the seeds.

SUMMARY.

1. The umbels are terminal.
2. The floral parts appear in centripetal succession.
3. The members of the same set arise simultaneously, and there is no confluence of primordia.
4. Glands are present near the axils of the sepals, bracts, and

leaves, in some species also on the midribs of the leaves; they are not in pairs, as stated by Engler and Prantl; and are not nectariferous.

5. The tube of the corolla seems to be of toral origin.

6. The adaxial surface of the corolla becomes papillose at the time of blooming.

7. The stamens are remarkable in the development of intercellular spaces.

8. The horn and hood are lateral outgrowths from the filament and composed largely of extremely loose tissue.

9. The fibrovascular bundle of the stamen loops into the hood to near its tip, the curvature beginning after the walls of the tracheids have formed spirals.

10. The elongation of the bundle to form the loop seems to take place by the stretching of the old tracheids and the formation of new ones at their sides.

11. The horn contains no vascular tissue.

12. The top of the "head," and not the functional stigma, is believed to be homologous with the stigma of normal angiosperms.

13. In general Corry's account of the formation of the caudicles, or connectors, and corpuscula is corroborated.

14. The generative cell divides near the tube nucleus, and in the normal manner. The division occurs before the formation of pollen tubes.

15. The pollen tubes from the same pollinium all enter the same ovary.

16. When the pollen tube enters the stigma the tube nucleus is behind the male cells, but it is doubtful whether any reported positions of nuclei in pollen tubes are beyond question.

17. The tube nucleus gets no further than the upper part of the ovary.

18. There is a single integument.

19. The nucellus is a single layer of cells enclosing the sporogenous row.

20. A single hypodermal archesporial cell forms a row of four megaspores without the formation of a parietal cell. Occasionally there is more than one archesporial cell.

21. In the formation of the megaspores the daughter cells do not divide simultaneously, thus perhaps giving a clue to the history of the abridgment of the process in some angiosperms.

22. The female gametophyte develops normally.

23. Double fertilization was observed in *Asclepias Cornuti*, one of the male cells fusing with the antipodal polar nucleus. This throws doubt upon the view that the attraction is due to near relation of the micropylar polar to the egg.

24. Fertilization may occur before or after the fusion of the polars.

25. A few tracheids were found in the ovules near the antipodals.

26. The fertilized egg rests until the endosperm has become sixteen-celled or more. It is surmised that some reported cases of endosperm division before fertilization may be due to mistaking fertilized for unfertilized eggs.

27. The pappus is composed of single-celled, uninucleate, epidermal hairs.

28. The double wall of the pod has its origin in the rupture of the parenchymatous tissue within the wall of the carpel.

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EXPLANATION OF PLATES XIII-XV.

All drawings $\times 23$ or more were made with a camera lucida. The lenses used were Zeiss compensating oculars in combination with Leitz dry lenses, a Zeiss dry achromatic adjustable, or a Zeiss $\frac{1}{2}$ apochromatic oil. The original drawings, for which the magnifications are indicated, are twice as large as the reproduction.

Asclepias tuberosa.

- FIG. 1. Longitudinal section through stem tip showing terminal umbel; *g*, glands; partly diagrammatic; $\times 30$.
FIG. 2. Hair from the epidermis of the calyx; $\times 390$.
FIGS. 3-4. Glands on the adaxial surface of the calyx; *p*, petal; *s*, sepal; $\times 555$.
FIG. 5. Top view of flower with all its organs removed except the sepals; *s*, sepal; *g*, gland; *p*, where petals have been cut; shows position of glands; $\times 48$.

Asclepias Sullivantii.

- FIG. 6. Part of longitudinal section through flower showing three glands in radial relation; *s*, sepal; *p*, petal; *b*, bundle; $\times 48$.

Asclepias Cornuti.

- FIG. 7. Basal portion of bract from umbel showing glands on adaxial surface; $\times 48$.

Asclepias tuberosa.

- FIG. 8. Gland from receptacle; *r*, receptacle; *p*, pedicel; $\times 390$.
 FIG. 9. Young stamen; *p*, pollinium; *b*, elongated elements preliminary to a bundle; $\times 48$.
 FIG. 10. Young stamen, older than *fig. 9*; *e*, end of vessel; *h*, beginning of hood and horn; $\times 48$.
 FIG. 11. Longitudinal section of stamen; *e*, end of vessel; *n*, horn; *d*, hood; *p*, pollinium; $\times 48$.
 FIGS. 12-15. Cross sections through *fig. 11* in planes indicated; *p*, pollinium; *c*, corpusculum; *w*, wing; *a*, alar chamber; $\times 94$.

Asclepias Cornuti.

- FIG. 16. Dorsal view of young stamen with concentric hood and papillate horn; $\times 23$.

Asclepias tuberosa.

- FIG. 17. Longitudinal section of stamen; hood and horn forming rapidly; $\times 23$.
 FIG. 18. Longitudinal section through mature stamen showing bundle looping far up into the hood; $\times 23$.
 FIG. 19. Section from *fig. 18* through hood (region indicated) showing aerenchyma; *s*, air space; $\times 203$.

Asclepias Cornuti.

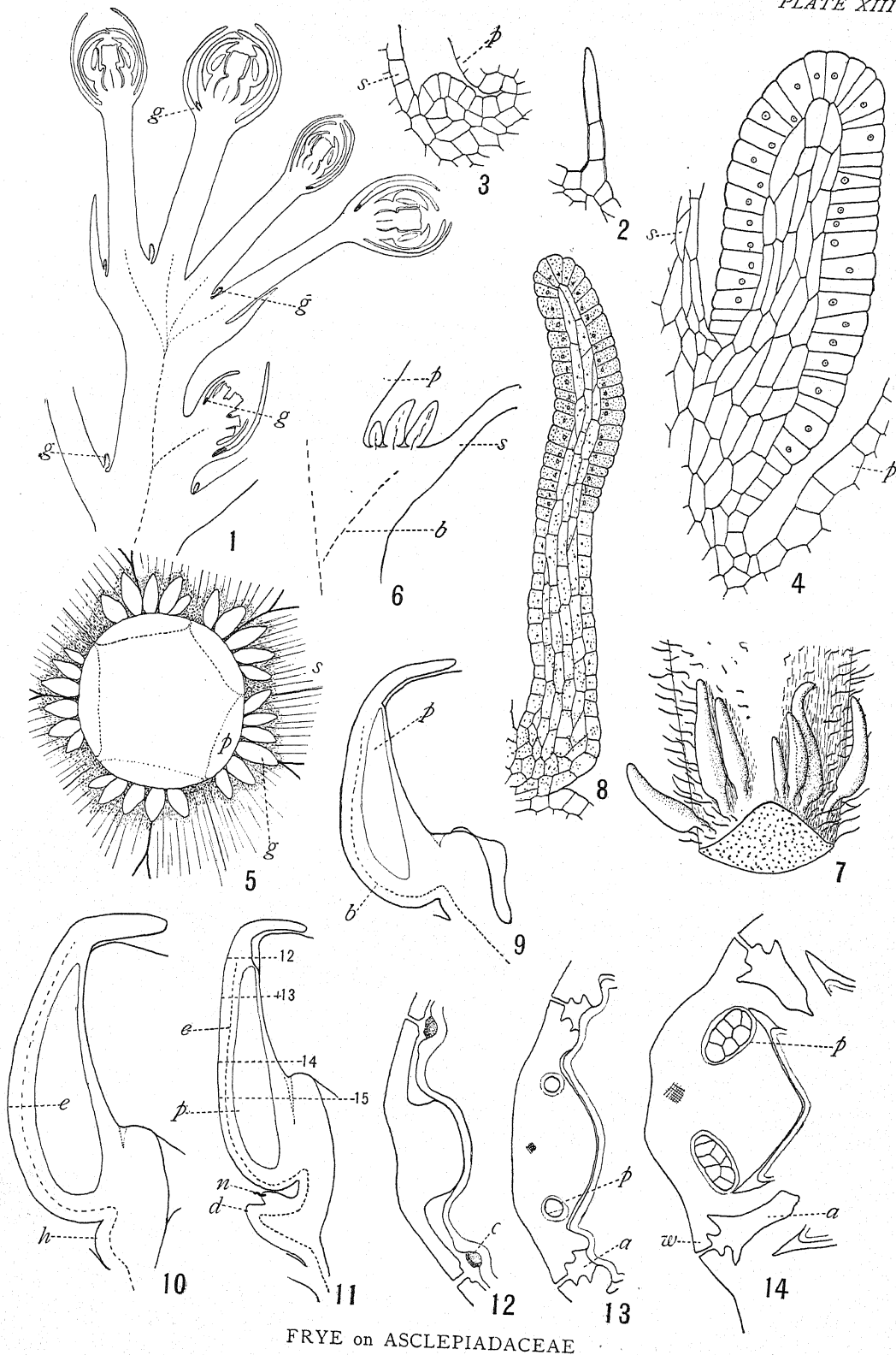
- FIG. 20. Part of flower with slice removed by tangential cut; *s*, stamen; *o*, ovary; *m*, mass arising from the staminal ring; $\times 23$.
 FIG. 21. Longitudinal section of basal part of stamen; *s*, sepal; *p*, petal; *n*, stamen; *m*, mass arising from staminal ring; $\times 94$.

Asclepias verticillata.

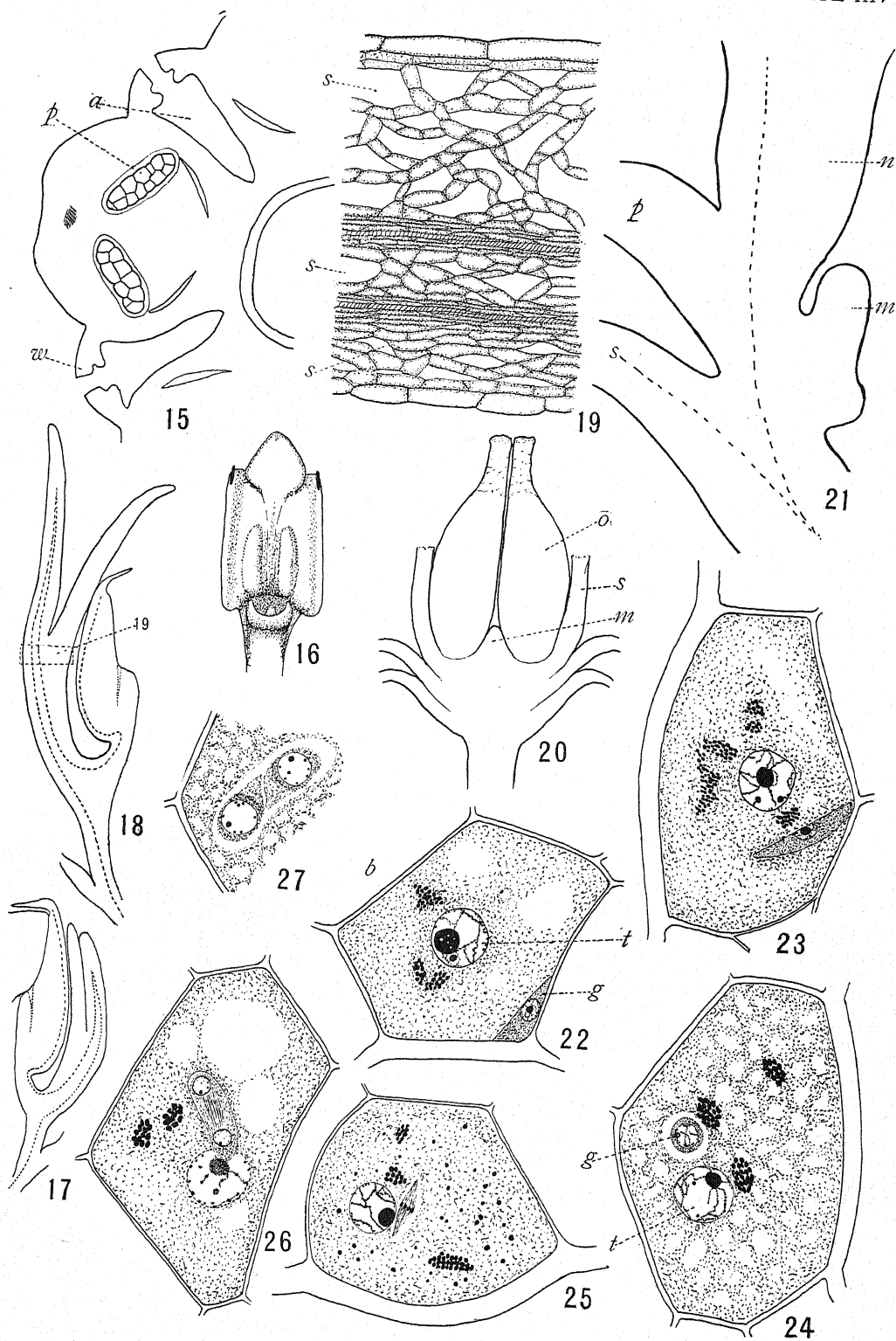
- FIG. 22. Pollen grain; *g*, generative cell; *t*, tube nucleus; *b*, undetermined bodies; $\times 1500$.
 FIG. 23. Generative cell leaving the wall of the pollen grain; $\times 1500$.
 FIG. 24. Generative cell before division, without a wall; *g*, generative cell; *t*, tube nucleus; $\times 1500$.
 FIG. 25. Division of generative cell, no wall about it; $\times 1500$.
 FIG. 26. Division of the generative cell; $\times 1500$.
 FIG. 27. Two male cells shortly after their formation; $\times 2200$.

Asclepias tuberosa.

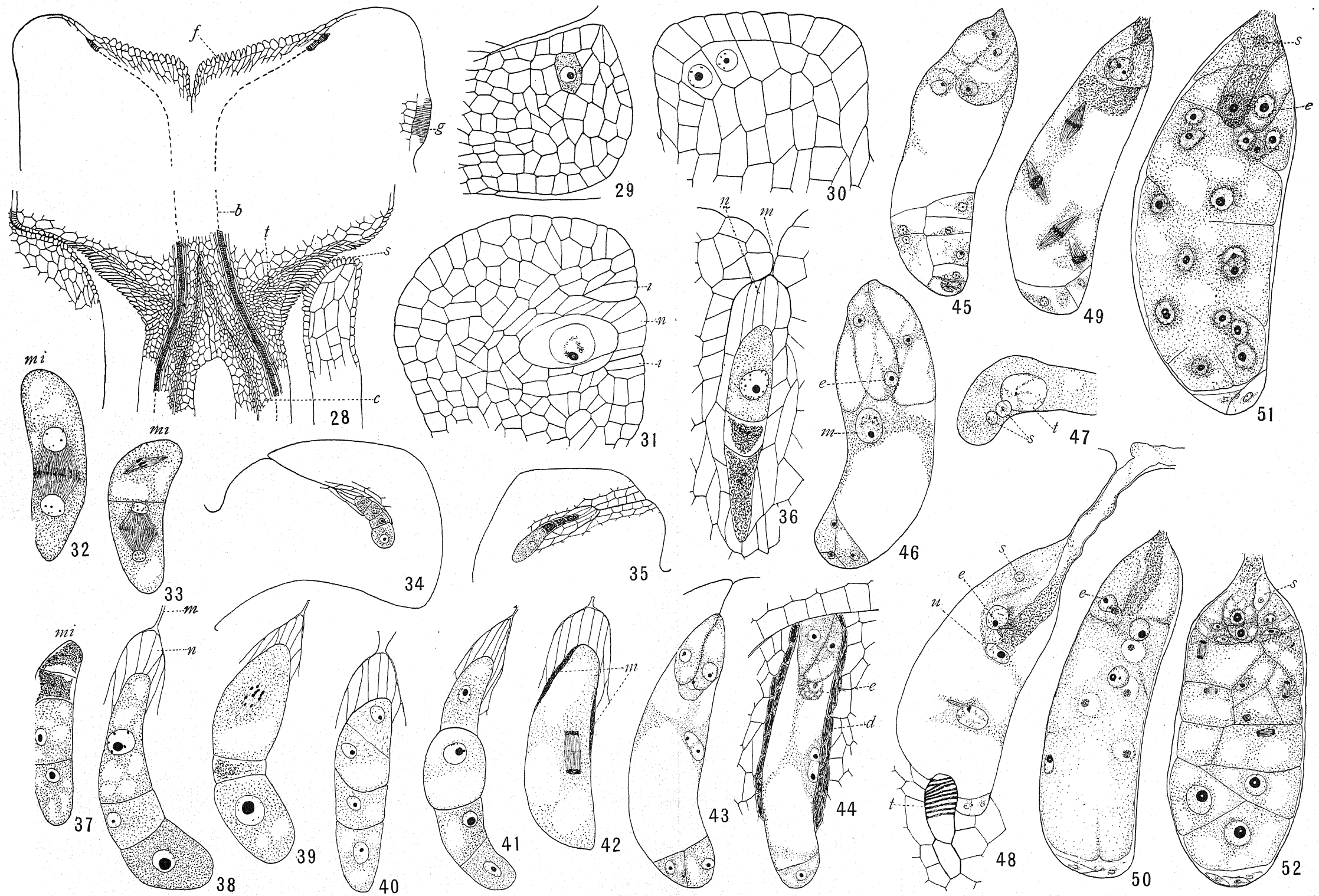
- FIG. 28. Longitudinal section of head; *s*, stigma; *c*, styler canal; *g*, glandular epidermis which forms the corpusculum; *f*, may be functionless stigma; *t*, conducting tissue; *b*, bundle; $\times 136$.
 FIG. 29. Ovule with archesporial cell; $\times 1275$.
 FIG. 30. Ovule containing two archesporial cells; $\times 2200$.



FRYE on ASCLEPIADACEAE



FRYE on ASCLEPIADACEAE



FRYE on ASCLEPIADACEAE

- FIG. 31. Ovule with integument just beginning to show; *i*, integument; *n*, nucellus; $\times 1500$.
 FIG. 32. First division of the mother cell; $\times 2200$.
 FIG. 33. Division of the daughter cells; $\times 2200$.
 FIG. 34. Row of four megaspores with the fourth surpassing the others; $\times 780$.
 FIG. 35. Disorganization of the first three megaspores; $\times 780$.
 FIG. 36. Domination of the first megaspore; *n*, nucellus; *m*, micropyle; $\times 2200$.
 FIG. 37. Row of four megaspores, two of which are about equally active; $\times 2200$.

Asclepias Sullivantii.

- FIG. 38. First daughter cell not yet divided; fourth megaspore enlarging; *m*, micropyle; *n*, nucellus; $\times 2200$.
 FIG. 39. First daughter cell dividing; third megaspore disorganizing; $\times 2200$.
 FIG. 40. Division of first daughter cell just completed; $\times 2200$.
 FIG. 41. Dominance of the second megaspore; $\times 2200$.
 FIG. 42. First division in the embryo sac; *m*, disorganized megaspores; $\times 2200$.

Asclepias tuberosa.

- FIG. 43. Normal embryo sac; union of polar nuclei; $\times 1500$.
 FIG. 44. Embryo sac which has reached the surface of the ovule; *e*, egg; *d*, disorganizing cells; $\times 1500$.
 FIG. 45. Eight antipodals; $\times 1500$.
 FIG. 46. Complete union of the polar nuclei before fertilization; *e*, egg; *m*, endosperm nucleus; $\times 1500$.
 FIG. 47. Tip of pollen tube entering the stigma; *s*, male cells; *t*, tube nucleus; $\times 2200$.

Asclepias Cornuti.

- FIG. 48. Double fertilization; *u*, micropylar polar; *e*, egg; *s*, synergid; *t*, tracheid; $\times 1500$.
 FIG. 49. Third division of the endosperm; $\times 1500$.
 FIG. 50. Eight-nucleate endosperm; *e*, egg; $\times 1500$.
 FIG. 51. Sixteen-celled endosperm; *e*, egg; *s*, synergid; $\times 1500$.
 FIG. 52. Two-celled embryo; endosperm massed about embryo; *s*, synergid; $\times 1085$.

THE ROOT-HAIRS, CAP, AND SHEATH OF AZOLLA.

R. G. LEAVITT.

(WITH PLATE XVI)

Roots spring from the prostrate floating shoots of *Azolla* in acropetal succession at the points of branching. They are from 2 to 5^{cm} in length, undivided, slender, and delicate, and in *A. filiculoides* and *A. caroliniana* are often, perhaps generally, provided with long outstanding hairs. These trichomes are peculiar in that they originate in the immediate neighborhood of the growing point, and from the first are marked out as cells designed for a distinct office. The way in which the hair initials, or fundaments of the root-hairs, are cut off, and the specialized character of the mature structures have not been described, so far as I am able to learn.¹ The material of *A. filiculoides* upon which Strasburger chiefly founded his classical memoir, "Ueber *Azolla*," presented a condition of the root quite unlike that which I have found in the same species. His plants had the roots enveloped in root-sheaths, and must have been entirely destitute of the trichome structures which form the principal subject of the present account. My own plants were somewhat variable, the roots occasionally being devoid of hairs. Yet the three lots of living material from independent sources which I have been able to see all exhibit the interesting process of hair formation to be described.

THE SHEATH AND CAP.

As the root-sheath and cap in the plants studied do not entirely conform to Strasburger's account, I shall take occasion to note the points of difference. For the sake of completeness Strasburger's exposition of the origin and early stages of the

¹Several references to the existence of these trichomes and one account of their peculiar distribution are to be found: WESTERMAIER and AMBRONN, Ueber eine biologische Eigenthumlichkeit der *Azolla caroliniana*. Verhandl. Bot. Verein. Provinz Brandenburg 22: 58. 1880; BERGGREN, S., Om *Azolla*'s prothallium och embryo. Lunds Univers. Årsskrift 16: 1878-1879.

root may be briefly recapitulated. In illustration two of his figures have been reproduced (*figs. 1, 2*).

The root of *A. filiculoides* begins with the differentiation of a large cell near the recurved tip of the growing stem beneath, at one side of the median plane, and in close proximity to an incipient lateral bud. This cell is the root initial (*fig. 1, R1*). It abuts internally upon cells from which later the vascular system of the stem originates. It is covered externally by a tabular cell, the root-sheath initial (*SI*), which subsequently divides once periclinally (*figs. 1, 2, S, S'*), and eventually in other directions. While at the very first the sheath is thus two-layered, the inner layer very soon disintegrates, and the mature sheath is only one cell thick. As stated above, this sheath in the condition of the plants seen by Strasburger envelops the root completely, though loosely, throughout life.

From the root initial (*R1*) a pyramidal apical cell is organized (*fig. 2, AC*). A single cap cell is cut off (*CI*), which afterwards, according to Strasburger, divides but once periclinally, a two-layered, adherent cap thus being instituted.

Fig. 3 of the accompanying plate represents a very young root. It is enveloped by a sheath comprising a single layer of cells. Shortly after the stage shown, this sheath in all the cases seen by me ceases to grow, and the root, continuing to elongate, bursts out. The old sheaths are to be seen as short collars, less than a millimeter long, around the bases of the roots.

The cap, as seen in *fig. 3*, is composed of two very similar cell layers (*c¹, c²*). In roots slightly more advanced a sharp differentiation of these layers is seen to have taken place. The outer becomes radially thicker, and its cells are vacuolated; while the inner remains relatively thin, and its cells are well filled with contents staining heavily like those of the body of the root. These differences forecast the very unlike histories of the two layers at a period a little later still, when the outer one, no longer growing longitudinally, becomes detached from the stem at the root's base, and being loosened from the root except at the tip is borne as a distinct cap; while at the same time the inner continues to grow and remains in connection with the root

trunk, like an epidermis (*fig. 4, c²*). After the root is about one-fifth grown the inner layer develops no further and is torn away at the base, to be carried downward as a cap in the further growth of the root, the upper part of the trunk therefore being left naked.

It may be worthy of remark that in its younger stage the root of *Azolla filiculoides* thus presents a state of things analogous to that in typical dicotyledons, since the superficial layer of the body of the root is derived from the calyptrogen—if we may so speak of the original cap segment (C1); whereas the mature root is like that of other vascular cryptogams and monocotyledons among flowering plants in exposing an unprotected cortex back of the root-cap.

In all cases examined by me there is an extra periclinal division at the apex of the inner cap (*fig. 4, D*).

In *Azolla caroliniana* I find that sheath and cap behave as stated for *A. filiculoides*, except that the second periclinal division (D) is absent.

THE ROOT-HAIRS.

In the majority of vascular plants root-hairs are formed by the external cells of the root in the region which is ceasing or has ceased to grow, where cell-division has been suspended and the tissues have become fixed. Here any or all of the cells without distinction of form, size, or contents may send out the organs of absorption. Only one exception was known to DeBary, that of *Lycopodium*, where the hair initials are set off in the still plastic epiblema not far behind the apex, and these, remaining short while the intervening cells elongate, alone produce tubular outgrowths. For the sake of comparison a figure of these hair initials and of the resulting structure in *Lycopodium lucidulum* is given (*fig. 11*). DeBary overlooked Bruchmann's observations² on the production of root-hairs in essentially the same manner in *Isoetes*, by the early establishment of special cells for the purpose.

The initials of the trichomes in the root of *Azolla filiculoides*

² BRUCHMANN, H., Ueber Anlage und Wachsthum der Wurzeln von *Lycopodium* und *Isoetes*. *Jenaische Zeitsch. Naturwiss.* 522. 1874.

(fig. 4, 11) arise within a belt of actively dividing cells, lying immediately under the inner root cap, not far from the apex, at an actual distance varying with the rate of growth of the terminal region. When that growth is most rapid the longest space intervenes between the apical cell and the youngest hair initials. As the root reaches the limit of its development, the hair-forming impulse travels downward until the apical cell itself is split into several parts, each one piliferous. The initials are formed in zones or partial zones. The mitoses to which they owe their existence are peculiar in that the axis of the mitotic figure in each case diverges more or less from the longitudinal axis of the mother cell, so that the resulting cell plate and wall lie somewhat diagonally (figs. 4, 8). Division thus gives two more or less wedge-shaped elements, of which the lower and slightly larger one is the hair initial.

This cell never elongates much in a direction parallel to the length of the root. The tube, which presently begins to grow out, turns toward the root apex (figs. 5, 6). As the hairs lengthen they at first lie appressed to the root and may be seen confined by the inner cap, which is now distended and pushed away from the root trunk (fig. 9). The whole cap structure is finally thrown off through the growth of the lower hairs, and the hairs themselves stand out strongly (figs. 12, 13). Their bases retain the wedge-form of the original hair initial.

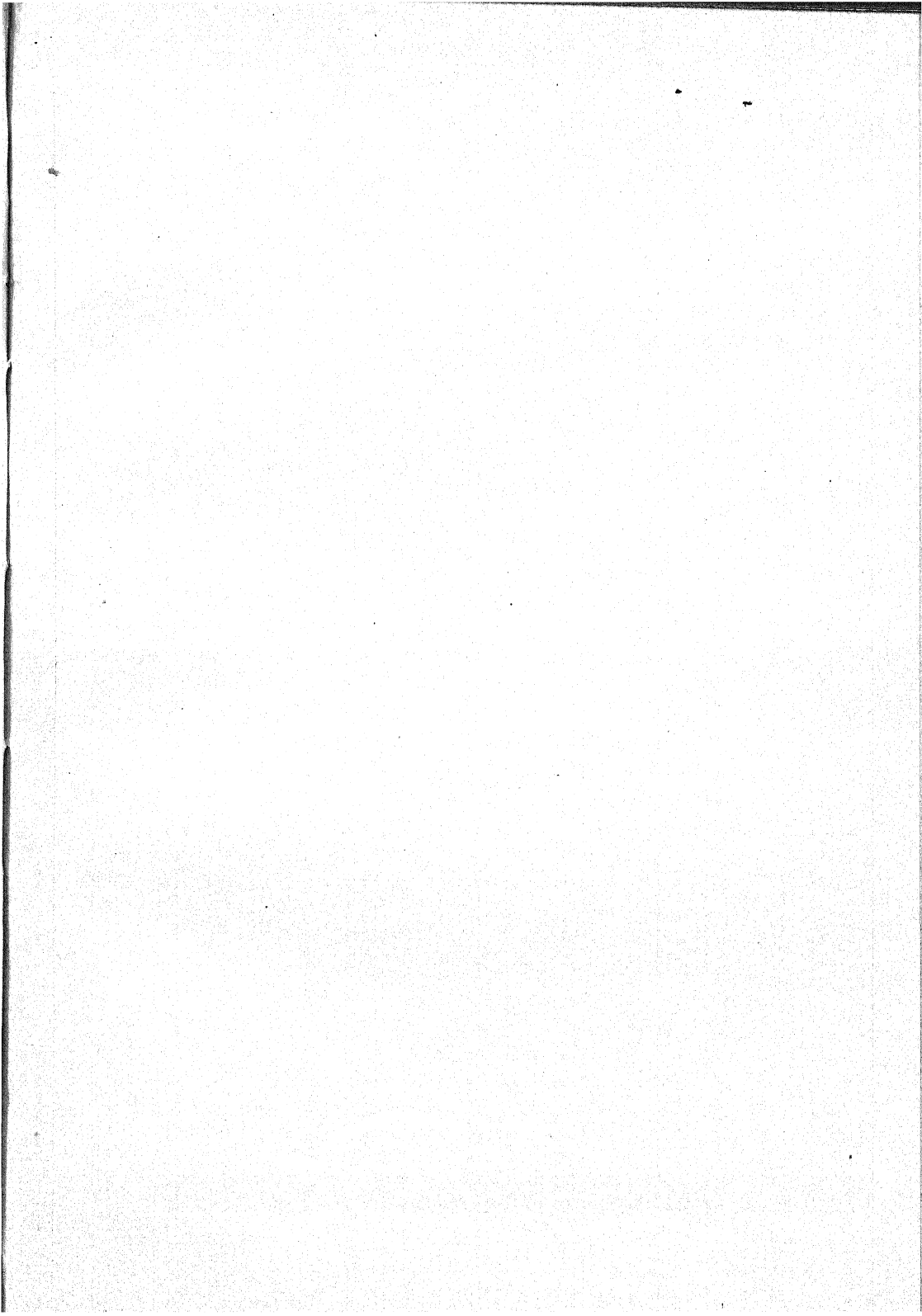
Soon after their organization the hair initials are to be distinguished from the cells with which they alternate by their contents, no less than by configuration, since they are more richly supplied with protoplasm (fig. 5).

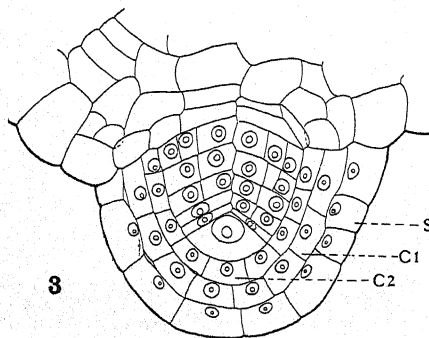
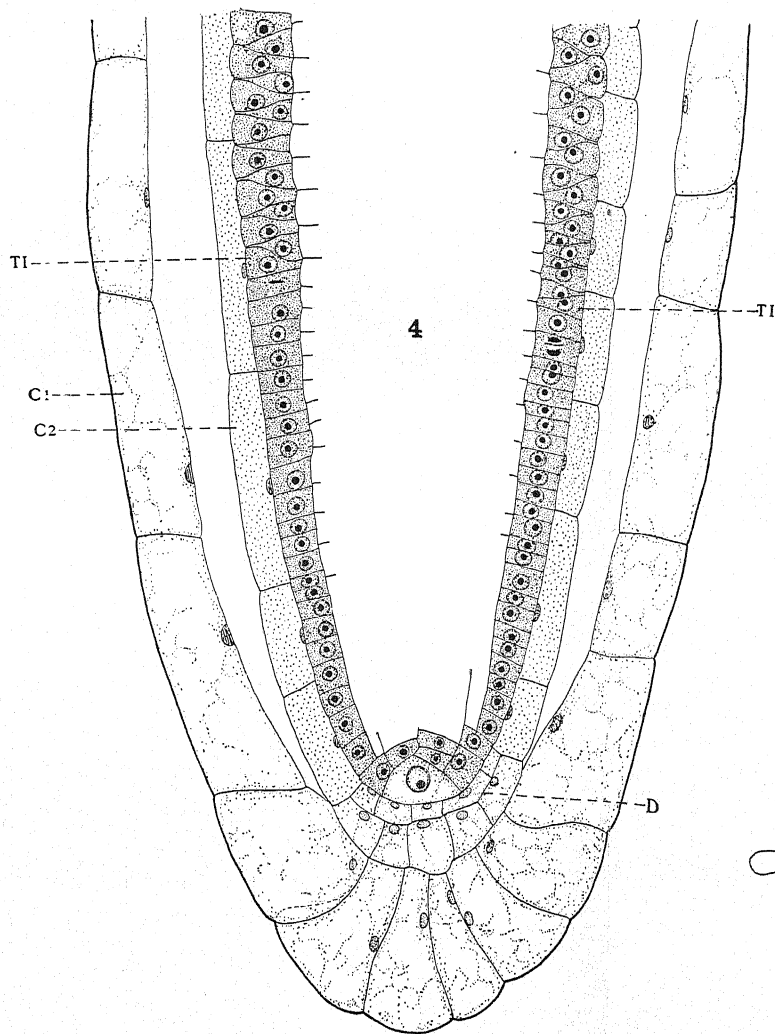
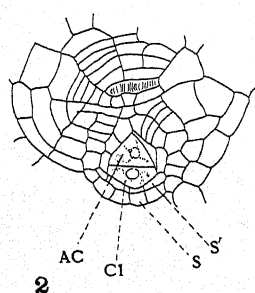
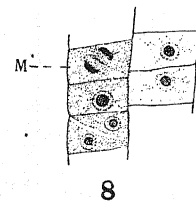
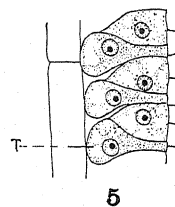
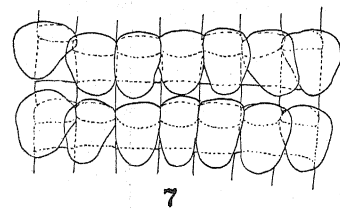
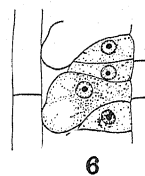
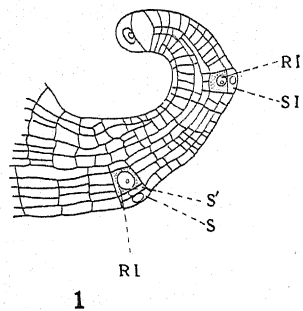
The lesser wedge-shaped cell produced simultaneously with the hair initial elongates and soon divides transversely (figs. 6, 9) once, twice, and often three times. The trichomes in each longitudinal cell row thus become separated by two, four, or eight cells. The intervening cells may be six, however. The number of divisions in neighboring rows may be different; and through the resulting displacements the original regularity of the hair zones is destroyed.

In the root of *A. caroliniana* the differentiation of the trichomes proceeds as in *A. filiculoides*.

The full grown hair may attain a length of about 2^{mm}. Its short base and the position with respect to the other elements of the epiblemma, which it occupies in consequence of its peculiar origin, give this sort of trichome a distinctive character (*fig. 10*). The fact will be appreciated upon comparison of the figures accompanying these notes with the root-hairs of ordinary dicotyledonous plants.

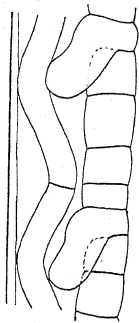
The superficial layer of the root trunk in *A. filiculoides* and *A. caroliniana* may be described as usually comprising, apart from the apical cell, four regions. Beginning with the youngest, these are: (1) a region of embryonic tissue in which the divisions are equating divisions; (2) a short zone where the divisions are differentiating divisions, giving rise ultimately to two sorts of members, trichomes and flat or prismatic cells; (3) a more extended belt, in which the cells of the second class again undergo equating divisions, and elongate; (4) a region of matured and fixed tissue, covering the greater part of the root. These regions represent successive stages in the genesis of the layer under discussion. An epiblemma with such a complex history is characteristic not only of *Azolla*—a highly specialized, terminal group—but of wide ranges of fern allies and monocotyledons, and of an isolated group of dicotyledons. My attention was first drawn to the matter by the similarity of *Sagittaria* and *Nymphaea* in this respect. I find a similar type of epiblemma in many members of Juncaginaceae, Potamogetonaceae, Aponogetonaceae, Naiadaceae, Alismaceae, Hydrocharitaceae, Juncaceae, Cyperaceae, Gramineae, Commelinaceae, Xyridaceae, Eriocaulaceae, Haemodoraceae, Zingiberaceae, Marantaceae, Orchidaceae; and in Nymphaeaceae (*Nymphaea*, *Nuphar*, *Brasenia*, *Cabomba*) alone among the dicotyledons examined. That the same trait is exhibited by such divergent groups as *Lycopodium* *Isoetes* (already noted by Bruchmann), *Selaginella*, and *Equisetum*—the last two instances seem to have been overlooked—shows that we have to do with an old element in vascular plants.



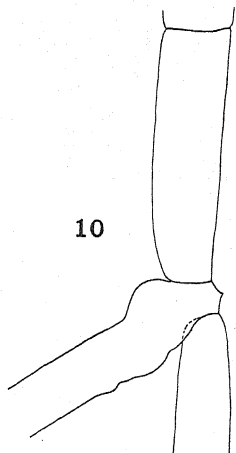


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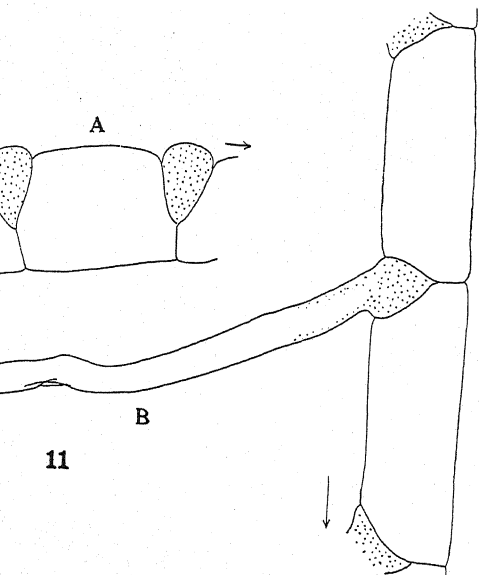
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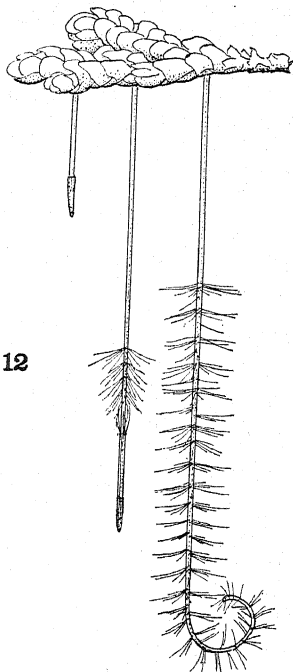
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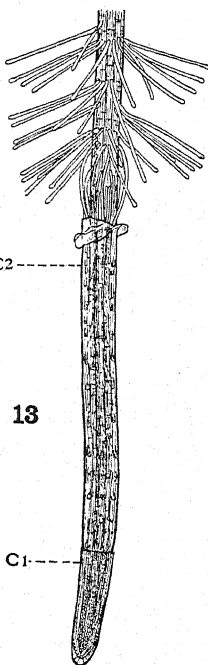
12



C2

13

C1



EXPLANATION OF PLATE XVI.

All figures except *figs. 1, 2, 12*, were drawn with the aid of the camera lucida.

- FIG. 1. Longisection of the growing apex of the stem in *Azolla filiculoides* (after Strasburger): RI, root initial; SI, sheath initial; s, s², segments of sheath initials; $\times 260$.
- FIG. 2. Fundament of the root in the same species (after Strasburger): AC, apical cell; CI, cap initial; s, s², outer and inner sheaths; $\times 260$.
- FIG. 3. Longisection of a young root of *A. filiculoides*; s, sheath; c¹, c² outer and inner caps; $\times 450$.
- FIG. 4. Longisection of the growing tip of a root of *A. filiculoides* (microtome section from material embedded in paraffin); D, periclinal division at apex of inner cap; c¹, c², outer and inner caps; TI, hair initial; $\times 450$.
- FIG. 5. Hair initials and intervening cells at the beginning of the growth of the hairs, about ten cell pairs removed from the oldest shown in *fig. 4*; $\times 450$.
- FIG. 6. First transverse division of intervening cell; $\times 450$.
- FIG. 7. Young root hairs seen in tangential section of the root, showing zonal arrangement; $\times 450$.
- FIG. 8. Origin of the hair initials; close of mitosis and forming cell-plate are seen at D; $\times 750$.
- FIG. 9. Young hairs in radial longisection, separated in the row by four intervening cells; $\times 300$.
- FIG. 10. Base of mature hair, between elongated epiblema cells; $\times 450$.
- FIG. 11. A, initials at the edge of the root-cap, and B, relatively young hairs near the tip of the growing root of *Lycopodium lucidulum*; the arrow shows the direction of the root apex; $\times 450$. A peculiarity of *Lycopodium* is that in most species the hair initials usually divide longitudinally, so that the hairs stand in groups of from two to four.
- FIG. 12. Habit of *Azolla filiculoides*; $\times 5$.
- FIG. 13. Terminal portion of root, showing cap and root-hairs; $\times 24$.

STUDIES IN THE FERTILIZATION OF PHYCOMYCETES.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY
XLII.

FRANK LINCOLN STEVENS.

(WITH PLATE XVII)

SCLEROSPORA, a genus of the Peronosporales, stands in a way intermediate between the Peronosporaceae and the Albuginaceae, a position that renders the problem of gametogenesis and fertilization of particular interest. This genus has heretofore received no cytological investigation.

The oogonia of *Sclerospora* average about 45 to 50 μ in diameter and are irregularly spherical in shape. The oogonial wall, even in young stages, is much thickened, thus forming a marked contrast with either *Peronospora* or *Albugo*. This wall averages from 3 to 5 μ in thickness, and stains readily with orange G.

Each oogonium contains approximately forty to fifty nuclei, borne in a cytoplasm differing in no essential particular from that of the oogonium of *Albugo* (*fig. 1*). The nuclei are relatively large and are rather fewer in number in comparison with the size of the oogonium than is usual with the other Peronosporales. The earliest stages of oogonium formation were not observed, so that it is not known whether the peculiar streaming of cytoplasm and the distortion of nuclei observed in *Albugo* (Istvánffi '95, Wager '96, Stevens '99) and in *Peronospora* (Wager '00) obtains here. As in *Albugo*, the nuclei in the young oogonium rapidly enlarge and pass into the spirem condition (*fig. 1*). From this stage on the process resembles that in *A. candida* (Wager '96, Davis '00, Stevens '01) more closely than in other Peronosporales, yet with certain marked differences. The mitosis is closely simultaneous, and may proceed until near metaphase without any indication of approaching zonation. When meta-

phase is reached, however, the nuclei are found arranged in an approximate circle around the region that is to become the oosphere (*fig. 2*). The arrangement is that of *A. candida* rather than of *A. Bliti*, and is such that no daughter nuclei can re-enter the oosphere region.

The exodus of nuclei is not complete, otherwise the oosphere would be enucleate and the condition would be like that of *A. Bliti*. One nucleus and, so far as my observation goes, one only remains behind with the coenocentrum, agreeing in this particular with *A. candida*. This nucleus may be seen there later in mitosis (*fig. 2*). This stage is directly comparable with that of *Albugo* represented by *fig. 14* in Stevens '01, with the difference that zonation is delayed longer in *Sclerospora* than in *A. candida*. The sequel of this condition is given in *fig. 3*, where one supernumerary nucleus is wandering toward the periplasm, leaving the female pronucleus in contact with or imbedded in the coenocentrum.

During the completion of the mitosis the ooplasm and periplasm become clearly differentiated, but as yet no plasmoderma exists. This process of differentiation has been termed zonation, and is here accomplished by a withdrawal of cytoplasm from the periphery of the oogonium, as in *Peronospora* (Wager '00, *fig. 2*) and *Albugo candida* (Stevens '01, *fig. 14*), not by an aggregation of separate dense regions, as in *A. Bliti* (Stevens '99, *figs. 59-61*).

At all times during oogenesis there is maintained in the oogonial wall contiguous to the antheridium an unthickened region (*figs. 1, 4, 5*).

In all the early stages of oogenesis the oosphere is seen to be eccentric, indeed the plasmoderma is usually almost in contact with that side of the oogonium adjacent to the antheridium (*fig. 4*). In cases of shrinkage it is also observed that the oogonial contents adhere firmly to this side of the oogonium, a phenomenon to be observed also in *Albugo*.

The coenocentrum is shown in *figs. 2-4*, and a trace of it still persists in *fig. 5*. In *Sclerospora* this structure is not so definite as in *Albugo candida* and *A. Tragopogonis*. Its highest differentiation is shown in *fig. 2*, where it consists merely of a region of

dense cytoplasm in the center of the oogonium, differentiated into two portions of varying density. In history and structure the coenocentrum agrees well with that of *A. Bliti*, with the exception that the central globule has not yet been demonstrated.

In function the coenocentrum serves to attract and to retain the female pronucleus, as in *A. Tragopogonis* and *A. candida* (Stevens '01), and in *Peronospora parasitica* (Wager '00). No evidence of nutritive function was apparent as in the case of the forms of *Albugo* just mentioned.

The mitosis in *Sclerospora* is in general of the type described for *A. Bliti* (Stevens '99). The spindle is intranuclear, the membrane persisting until metaphase. No centrosomes or polar radiations were seen. Chromosomes were not counted with accuracy, but they are few in number, probably four.

The antheridium in *Sclerospora* is usually very small, and is closely appressed to the oogonial wall (*fig. 4*). Usually it is impossible to distinguish the antheridial wall from the oogonial, and very frequently the thinning of the oogonial wall gives the antheridium the appearance of being imbedded in it. The antheridial nuclei enlarge simultaneously with those of the oogonium, and undergo mitosis. No receptive papilla was seen, and this peculiar structure may be lacking in the genus.

Communication is opened between the antheridium and the oogonium by the bulging and eventual rupturing of the oogonial wall at the thin point between these organs. The edges of the ruptured wall thus extend inward. The antheridial tube, which is soft and gelatinous, penetrates the oosphere, discharging its contents before it reaches the center (*fig. 4*). The track of the antheridial tube remains in evidence for some time as a denser region in the cytoplasm.

The male pronucleus is slightly smaller than the female and is more ovoid in form (*fig. 7*). It migrates to the female and fuses with it, but the fusion was not studied critically owing to the smallness of the nuclei.

The oogonial wall, as stated above, is much thickened even in the youngest oogonia, and it does not change in dimensions

as it matures. With zonation the regions of ooplasm and periplasm are clearly mapped (*fig. 3*), and with the opening of the antheridial tube the plasmoderma appears. The oospore wall now develops rapidly, first appearing as a clearly defined wall (*fig. 5*), then rapidly increasing in thickness (*fig. 6*). As the oospore wall thickens the oogonial wall collapses in irregular folds (*fig. 6*), and the periplasm and periplasmic nuclei degenerate. The protection afforded by these two thick walls appears to hinder seriously the penetration of killing and fixing fluids or subsequent manipulation, and no good preparations showing nuclei were obtained at any stage after the second wall was far developed.

GENERAL CONSIDERATIONS.

The general bearing of the cytological evidence on the relationship of *Sclerospora* is to emphasize its affinity to the Peronosporaceae rather than to the Albuginaceae, and to indicate its specialized rather than primitive character. The general course of development of both antheridium and oogonium, and the behavior of the periplasm are as in the whole group Peronosporales. The mitosis in both of these organs has been shown by Trow ('99, '01), Hartog ('95), Wager ('96, '00), Miyake ('01), Stevens ('99, '01), King ('02), and others, to be characteristic of both Saprolegniales and Pernosporales.

The mode of zonation in *Sclerospora* is not that of the Saprolegniales (Trow '01, Miyake '01, Hartog '95), nor of the primitive Albuginaceae (Stevens '99). It does agree closely, however, with the Peronosporaceae. While the zonation of *A. candida* agrees with that of the Peronosporaceae, *Sclerospora* shows by the nature of its coenocentrum, which in structure, history, and function is clearly like that found in *Peronospora*, its closer relationship to the Peronosporaceae than to any Albugo.

The conclusion regarding the relationship of the genus, purely from cytological standpoint, coincides with that drawn from the gross study of asexual spore-bearing organs, and emphasizes the relationship of this genus to *Peronospora*, of which genus it was once considered a member.

Sclerospora, as shown by the combined evidence of the

double investment of its oospore, the character of its conidio-phores, and its cytology, probably separated early from the main line of the Peronosporaceae, at a time much later than the divergence of the Albuginaceae from the Peronosporaceae.

It is a pleasure to acknowledge indebtedness to my wife for the plate accompanying this article.

COLLEGE OF AGRICULTURE AND MECHANIC ARTS.
Raleigh, N. C.

LITERATURE CITED.

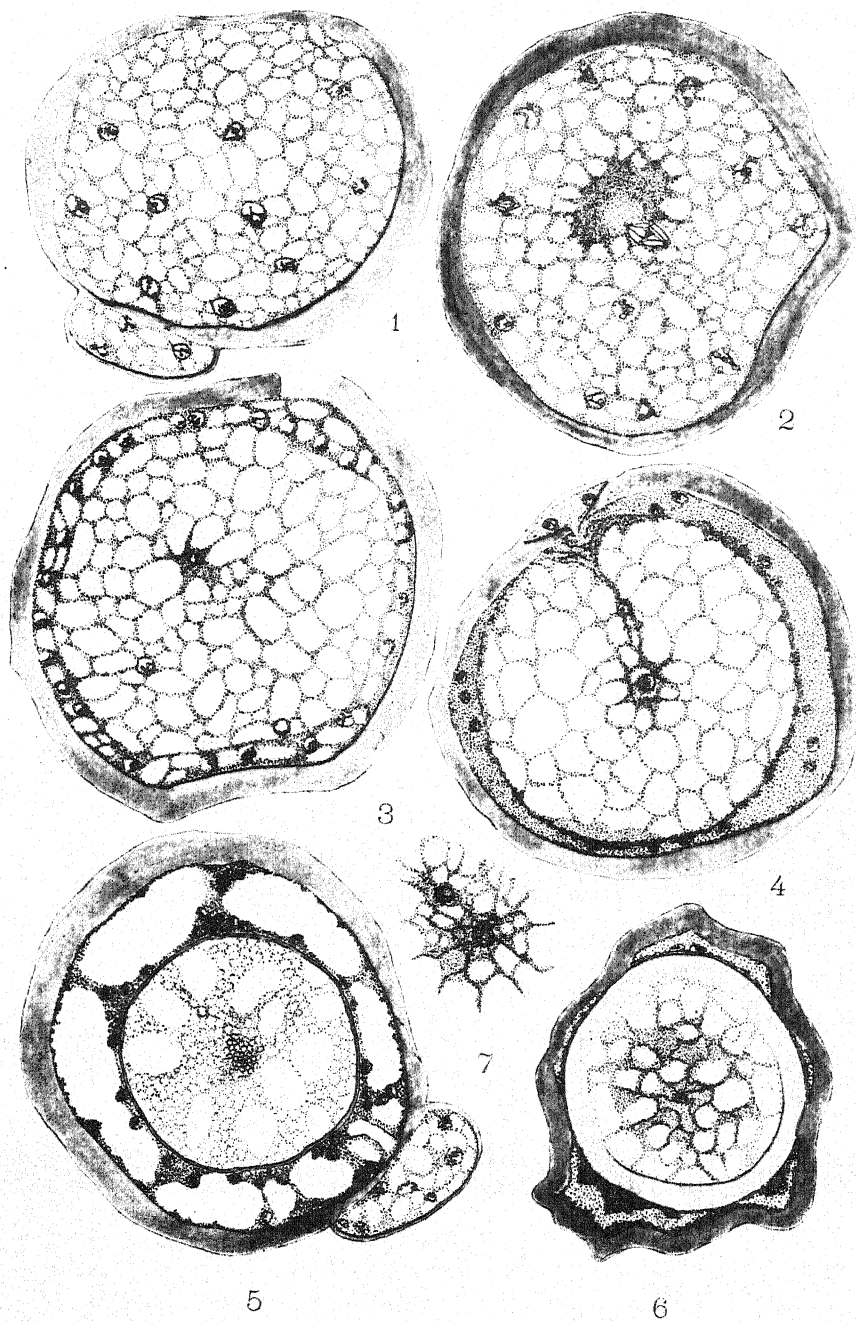
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WAGER, '96: On the structure and reproduction of *Cystopus candidus* Lev. Ann. Botany 10 : 295-342.
——— '00: On the fertilization of *Peronospora parasitica*. Ann. Botany 14 : 263-273.

EXPLANATION OF PLATE XVII.

All figures are from material killed in chrome-acetic acid and stained with Flemming's triple stain. The figures were sketched with the aid of an Abbé camera, using the Leitz $\frac{1}{2}$ objective, ap. 1.30. The original drawings gave an enlargement of 1790 diameters, and have been reduced one-third in reproduction.

FIG. 1. Young oogonium and antheridium; nuclei in spirem; wall thickened and staining darkly with orange G.

FIG. 2. Nuclei migrating to periphery; coenocentrum well developed; one nucleus in metaphase anchored to it; peripheral nuclei in advanced prophase.



STEVENS on SCLEROSPORA.



FIG. 3. Zonation ; mitosis completed ; one daughter nucleus remaining with coenocentrum, the other passing to periplasm.

FIG. 4. Fertilization ; antheridial tube ruptured, emptying one nucleus into oosphere ; female nucleus resting in coenocentrum.

FIG. 5. Oospore wall forming ; periplasm and periplasmic nuclei degenerating ; remains of antheridium and trace of the tube in periplasm.

FIG. 6. Winter condition.

FIG. 7. Pronuclei just before fusion.

NOTES ON SASSAFRAS.

EDWARD W. BERRY.

(WITH PLATE XVIII AND FOUR TEXT FIGURES)

MONOTYPIC genera are always of more than ordinary interest, especially when they have a geological history. Our common *Sassafras* proves no exception to this statement. Ranging in size from a bush to a tree 125 feet high and with a trunk seven feet in diameter,¹ distributed from Massachusetts west to Iowa and Kansas, and from Ontario and Michigan south to Florida and Texas, ascending to 3500 feet above the sea level in Virginia, it is equally at home in the dry sandy soil of some of our roadsides or in rich woodlands. Belonging to a cosmopolitan tropical family of over 900 species, some of which were well known in the most ancient times, and many of which are of considerable economic and medicinal value (camphor, cinnamon, etc.), the common *Sassafras* was first described by Linnaeus as *Laurus Sassafras*,² in allusion to the common Spanish name. It is with the leaves that we are principally concerned, and it is interesting to note that all of our manuals speak of them as "entire or three-lobed,"³ or as "entire to three-lobed,"⁴ although in reality they are often four or five-lobed, not occasionally, but regularly so, some trees having all their leaves similarly four or five-lobed, while I have occasionally found specimens with six lobes. Most authors, lacking the time or material for verification, repeat previously published statements which are often misleading. Believing that there is no organ whose variations are not without significance, especially in view of the importance recently assigned to the statistics of variation, I have examined several hundred leaves of *Sassafras* of all ages, from trees of all sizes, and from all positions; from saplings, shoots from trunks, barren and flowering branches, etc. A discussion

¹ BRITTON, *Illus. Fl.* 2: 97. ² *Sp. Pl.* 371. 1753. ³ WOOD, *Classbook*, p. 620.

⁴ GRAY, *Manual*; CHAPMAN, *Southern Flora*; BRITTON, *Ill. Flora*.

of the variations, necessarily brief, is followed by an examination of the numerous fossil leaf-forms which have been referred to this genus, and their probable relations are pointed out.

SIMPLE LEAVES.⁵—Greatest length 190^{mm}, greatest width 107^{mm}; shape varying from lanceolate, through ovate lanceolate, to almost orbicular; tip truncate, rounded, or cuspidate; lateral margins ascending at an angle of about 45° at their base; base narrow and more or less decurrent on the petiole, especially in young leaves; texture from membranaceous to coriaceous. In texture, however, as well as in general form and character of venation, the leaves of a single tree proclaim their relationship, so that particularly pointed lobes or the reverse, broad short leaves or the reverse, very thin or very thick leaves, whether simple, bilobed, trilobed, or multilobed, all have the same aspect.

Bud leaves are always narrow, with ascending laterals forming an angle of 30° or less; somewhat older leaves, about June 1, when they are about 60 or 70^{mm} in length, had the primaries and secondaries indistinguishable in 68 per cent. of the leaves examined, in numerous older leaves the primaries are only to be distinguished by their greater length, are rarely opposite, and sometimes have a pair of secondaries below them nearly as large. There were an equal number of primaries and secondaries on each side in 60 per cent. of the leaves examined.

BILOBED LEAVES.—The bilobed leaves are more variable than the simple leaves, varying in outline from oblong-lanceolate to nearly orbicular. The lateral lobe may be broadly rounded or even reduced to a small blunt protuberance, or it may be narrowly acute, extending at almost right angles, or directed upward and not extending above the basal half of the leaf; or it may extend as far as the tip of the main blade and nearly equal it in size. The sinus varies from a slight wide depression extending only one-eighth of the distance to the midrib, to one extending three-fourths of the distance, and wide and obtuse or narrow and acute. Venation, of course, is inequilateral. Eighty per cent. have first secondary lower, and primary generally higher on the lobed side.

⁵ It is well to note that any statements made here refer only to the series I have examined.

MULTILOBED LEAVES (*Plate XVIII.*)—It is among the 3-5-lobed leaves, however, that the greatest variation prevails. In the trilobed forms the lobes vary from broadly obtuse to narrowly acute (rarely retuse), from mere lateral prominences to broad lobes extending nearly to the top of the leaf. They

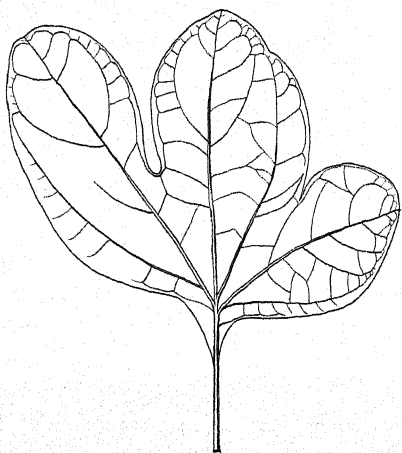


FIG. 1.—Abnormal leaf of *Sassafras*; reduced two-thirds.

may never extend above the basal half of the leaf, although directed upward, or they may extend at right angles, or even occasionally be recurved. They may be orbicular or long narrow fingers enclosing a deep rounded sinus which extends nearly to the midrib. In a leaf 165^{mm} long and 127^{mm} wide the sinus extended to within 3.50^{mm} of the midrib. Out of 102 leaves considered of sufficient interest to sketch, 45 were approximately bilateral, and 57, or

about 56 per cent., were more or less greatly inequilateral. While this is not a natural proportion, as only divergent forms were preserved, it shows the wide range of variation from a leaf with one lobe acute and extending at right angles a distance of but 7^{mm} from the wide shallow sinus and three-elevenths from the base, the other oblong and ascending, extending nine-elevenths of the distance to the tip, and enclosing a deep, narrow sinus; to leaves in which one half is nearly the exact counterpart of the other. The base varies from narrowly ascending in the younger leaves to nearly truncate; all of the leaves seen, however, are more or less decurrent. The anomalous leaf shown in *fig. 1* is worthy of special mention as having an almost palmate venation, there being four and the indication of a fifth possible primary. The right hand sinus runs to a narrowly acute point, and entirely lacks the marginal venation so characteristic of *Sassafras*.

The bases of the primaries may be from 5-7^{mm} apart or they

may be opposite; they may form an acute angle with the midrib but 6 or 7^{mm} from its base; or they may not branch from the midrib until one-fourth the distance to the tip is traversed (one example four-fifths and one three-elevenths).

The typical five-lobed leaves, excluding those with four lobes, which are similar with the obliteration of the sinus of one of the lobes, or are the typical trilobed leaves with a small extra lobe on either side of the terminal or lateral lobes, sometimes even having six lobes (*fig. 4*), are strikingly handsome leaves and would hardly be taken for Sassafras leaves by even a trained observer. They undoubtedly represent a great development laterally of the typical trilobed forms with the additional small lobes (*fig. 2*), all the

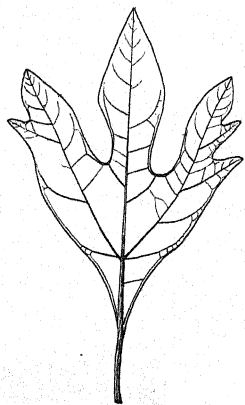


FIG. 2.—Abnormal leaf of Sassafras; reduced two-thirds.

lobes becoming greatly broadened and somewhat orbicular in outline. They are constant on some small trees which I have had under observation, and may represent the result of a superabundant food supply, as they all grew in rich soil of open woodlands. These leaves are nearly orbicular in outline, a

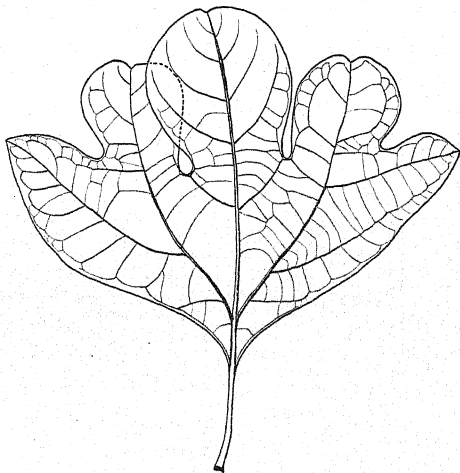


FIG. 3.—Abnormal leaf of Sassafras; reduced two-thirds.

large specimen measuring 156^{mm} in length by 200^{mm} in breadth (*fig. 3*), and consist of a central lobe and a pair of lateral lobes on each side, all nearly equal in size and separated by deep spatulate sinuses. The tips range from acute to rounded,

and in several instances are even retuse. The base of the leaf is in all cases decurrent and the angle of divergence of the ascending margins never exceeds and seldom equals 45° . While the comparative size of the lobes varies somewhat, the leaves are approximately bilaterally symmetrical. This form seems to have

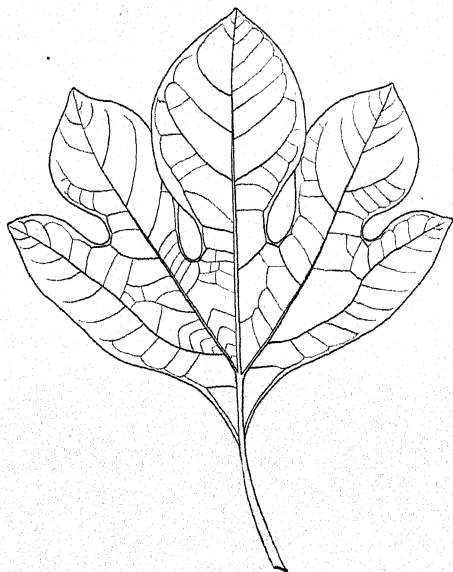


FIG. 4.—Abnormal leaf of *Sassafras*; reduced two-thirds.

escaped attention heretofore, and none of the fossil forms referred to this genus resemble it in the least except *S. platanoides*. An ancient form which resembles these five-lobed leaves in outline is Fontaine's *Araliaephyllum obtusilobum*; the latter, however, has thicker veins and the lateral lobes are not so extensively developed; and the lateral which runs from the primary to the extra lobe is inserted much nearer the base than in the modern leaves.

The venation of the modern leaf is uniform in its variation. Safe rules for guidance in determining fossil forms would be the following: The primaries are opposite or sub-opposite (while this is not strictly applicable to the simple leaves it seems to be general in the lobed ones); they branch from the midrib a considerable distance above its base, thus differing from *Aralia*, *Cissites*, *Platanus*, etc.; the base is never enlarged to form basal lobes as it is in *Menispermites*, *Araliaephyllum*, *Protophyllum*, *Aspidiophyllum*, *Platanus basilobata*, etc.; margins are entire; obviously, if any of the ancestral forms were dentate, this character would reappear occasionally in their descendants (all known Lauraceae have entire margins). A somewhat constant character in *Sassafras* leaves is the venation of the basal portion of

the blade. A pair of secondaries or tertiaries branches from the petiole at the juncture of the leaf-blade and forms its ascending margins, becoming slightly separated where the latter curves outward—a short distance above the base of the primary the lowest lateral curves toward the margin; just before reaching the margin it forks, the lower short branch joining the marginal vein and the other branch curving upward; the former together with the marginals form a rough inverted isosceles triangle, whose base is usually approximately on a level with the point of insertion of the primaries or slightly higher. This arrangement occurs in all the normal leaves examined by me, numbering several hundred, and in the abnormal forms it occurs in all but seven specimens out of 229. I fail to find this feature in any of the published figures of fossil forms, but it is a character which would be easily obliterated or overlooked, as marginal veins would not be distinguishable from margins unless they were of considerable size or the matrix were exceedingly fine-grained. A remarkable character of the modern lobed leaf, first pointed out by Lester F. Ward⁶, are the marginal veins at the bottom of the sinuses.

In the normal trilobed leaf about half the distance from the lateral primaries to the tip of the leaf is traversed before the first pair of secondaries branch from the midrib; the interval is filled with cross and horizontal veins which belong to the tertiary system; the secondaries in question leave the midrib at usually a wide angle, and curving upward pass directly to the sinuses. Here they are not lost but fork at a wide angle, often 160° , the two branches following the margins of the sinus for more or less distance until they leave them to join the branches given off from the primaries below and the next pair of secondaries above. This is nearly a constant feature of the modern leaf, recurring in substantially the same manner in all forms of the leaf, whether 2, 3, 4, 5, or 6-lobed. In leaves in which the sinuses approach the midrib closely there are numerous tertiary veins passing directly from the midrib to the sinus and from the primary to the sinus, joining its marginal vein. Just what purpose is served by this marginal vein in the economy of the leaf is difficult to

⁶Bull. 37, U. S. Geol. Survey, p. 61.

say. It might serve to strengthen the leaf and prevent tearing where the lobes are large; at any rate it is an acquired feature the origin of which is shown in some specimens and serves to prove that the ancestral leaf was simple, and not lobed as Ward holds; it also rules out the contention that ancient leaves lacking this arrangement are not forms of *Sassafras*, as we would hardly expect this character in the ancestral forms becoming lobed.

This marginal vein at the bottom of the sinus was lacking in fifteen single instances, and a secondary sinus lacked it in four instances out of a total of 201 leaves examined especially because of their diverse lobation. In nature it is undoubtedly a nearly constant character. In some cases the secondary which runs to the sinus is continued into the upper or the lateral lobe, and a tertiary from the midrib unites with one from the primary, then running to the sinus in the usual manner; or it may be a branch from the secondary together with one from the primary which forms the margin; the latter, however, is always thickened irrespective of the system to which it seems to belong. I have collected several specimens in which the secondary forks before reaching the sinus, the branches striding it after the manner which usually obtains in the lobed leaves of a variety of genera, the branches connecting with the branches from the next secondary above and with those from the primary below.

No fossil American *Sassafras* has, or at least shows, this peculiar marginal venation, but it occurs in a European representative of this genus according to Ward⁷. The secondary seems to run to the sinus in *S. bilobatum*, *S. platanoides*, and in some specimens of *S. progenitor*. The form which Lesquereux describes as *Aralia acerifolia*⁸ approximates this style of venation as does also the leaf referred to *Lindera venusta*⁹, which leaf Knowlton refers to Benzoin.

On general principles we would expect the ancestral *Sassafras* to have had simple, lanceolate, or ovate-lanceolate leaves with entire margins. Not only is this a rule among the Laura-

⁷ *Sassafras Ferretianum* Mass., from Senegal. Fl. Foss. de Seneg. pl. 12. fig. 1.

⁸ Cret. and Tert. Fl. pl. 49. fig. 5. ⁹ See Fl. Dak. Group, pl. 16. figs. 1-2.

ceae, but even in the existing *Sassafras*, aside from some striking exceptions, the majority of the leaves on full grown trees are simple. It is doubtful if we shall ever know these ancestral forms as such even if found, as they will probably be described as *Laurus*. In all probability the ancestral forms of all the dicotyledons were developed in an area remote from localities where fossilization was going on, as suggested by MacMillan¹⁰. In *Liriodendron* the variation from the oldest to the youngest leaf on a shoot from the modern form epitomizes the phylogeny in a general way. If the like holds good in *Sassafras* it would hint at an ancestor with trilobed leaves, for in all the forms which I have examined there seems to be a somewhat constant gradation from the outer (older) two or three-lobed leaves, through the simple lanceolate or ovate-lanceolate bud leaves, to the spatulate-ovate bud scales, which persist to form the involucre of the flower cluster.

Paleobotanists associate the name *Sassafras* with lobed leaves, and I do not know of a single specimen of a simple leaf which has been described as *Sassafras*, although several leaves referred to other species might easily be forms of *Sassafras*, as for instance *Cinnamomum Heeri* Lesq. from the Dakota group¹¹. Premising this much what shall we say of the relations of the numerous fossil species of bilobed and trilobed leaves which have been referred to this genus, ranging in time from the Potomac formation upward? While some are undoubted forms of *Sassafras* and have always been known as such, others are just as undoubtedly not forms of *Sassafras* at all. Very diverse opinions have been advanced as to their proper position. Saporta questions all of the references of trilobed leaves to *Sassafras*, and suggests their affinity with *Aralia*, pointing out their resemblance to the Central American genus *Oreopanax*. *Araliopsis* has always been a convenient shelf on which to place these leaves, but it seems to me that such references are altogether unsatisfactory. Lester F. Ward¹² is of the opinion that it is

¹⁰ The probable physiognomy of the Cretaceous plant population. *Amer. Nat.* 27: 336. 1893.

¹¹ *Fl. Dak. Group*, p. 105, *pl.* 15. *fig.* 1.

¹² *Proc. Nat. Museum* 11: 39-42. *pls.* 17-22. 1888.

doubtful if any of the so-called *Sassafras* leaves from the Dakota Group are correctly named, and says that they will eventually be recognized as interrelated with *Platanus*. While there is much in favor of this view, especially in the case of some species (which will be considered in their proper place), it is too sweeping and will have to be qualified.

The existing species is noted for its variable leaves, which may be simple, 2, 3, 4, 5, or 6-lobed, and we quote from Lesquereux to show with what certainty he regarded some of his determinations. In speaking of *S. platanoides*, he asks "is it referable to *Sassafras*, *Aralia*, or *Platanus*?"¹³ *S. mirabile* he originally referred to *Platanus*; he asks "what is *Aspidiophyllum dentatum*, *Sassafras* or *Platanus*?" He says of *S. dissectum* that it "has in the division of the lateral lobes the character of *Aralia*, while by its size and general outline it is a *Platanus*, and still further by the basilar prolongation and dentate lobes it is merely a variation of *S. mirabile*, or in the still farther development of the base it approximates *Aspidiophyllum* and *Menispermites*; in fact incomplete specimens of *Aspidiophyllum* which lack the basal portion have generally been referred to *Sassafras*."

I propose to consider the various fossil species in the light of the modern leaf, and believe that the relations which are suggested in the following pages, while necessarily imperfect, are more natural than any treatment heretofore accorded them. While all attempts at phylogeny are necessarily hypothetical, especially when dealing with only one set of organs, such as leaves, and many of these scattered and fragmentary, I have not hesitated to theorize, believing that such attempts when founded on careful study not only serve to coordinate existing knowledge of the group but furnish starting points for new lines of investigation. I exclude for the present any consideration of the species from Europe or the Arctic region.

The oldest species referred to this genus in America are Fontaine's three Potomac species as follows:

SASSAFRAS PARVIFOLIUM may be dismissed with the statement that there is nothing about this fragment of a small leaf to war-

¹³ Fl. Dak. Group. p. 231.

rant its reference to *Sassafras*. Of rare occurrence, it probably represents a young leaf of some unrelated species, or possibly of the leaf which Fontaine describes under the following name.

SASSAFRAS CRETACEUM HETEROLOBUM resembles *S. cretaceum obtusum* Lesq. from the Dakota formation and the Cheyenne sandstone, but is considerably smaller and with more pointed lateral lobes. We may class it with the doubtful forms referred to *Cissites*, its general outline (except the pointed lobes) being quite similar to *Cissites salisburiaefolius* Lesq. from the Dakota formation, which species Lesquereux determined as *Populites*, *Sassafras*, and *Cissites* successively. Or we may consider it as related to the ancestral form from which *Platanus*, so extensively developed in the succeeding strata, was developed. At any rate, I see no reason why it should be considered a species of *Sassafras*.

SASSAFRAS BILOBATUM.—While the outline of this leaf does not exactly conform to any modern bilobed *Sassafras* leaf known to me, it is nearer the latter than it is to any other leaf. The right-angled sinus with straight sides and running to a point is also a feature not seen in the modern leaf. In the latter, when the sinus runs to a point it is narrow and deep; and when it forms a right angle it is curved and the resulting lobe is generally obtuse and but slightly produced. We have characters which ally this ancient leaf to *Sassafras* in the decurrent base; the sub-opposite primaries, as they usually are in the bilobed leaves of the existing *Sassafras*; the position of the secondaries; and especially in the secondary running to the sinus, a feature we would hardly expect to find in so primitive a leaf. We would consider the bilobed leaf as a more ancient type than the trilobed form, and removed from the ancestral simple leaf by a series beginning with leaves with but a slight depression marking the position of the future sinus, and a slightly produced obtuse lobe, through forms partially paralleled in the modern leaf, in which these features were more and more emphasized. Just why the leaf became lobed is largely conjectural. The primaries form a more acute angle with the midrib than do the secondaries, especially in the simple leaves; they are the first and largest arteries branching from the midrib; in the growing leaf

they are carried upward, while new laterals are added toward the tip of the blade. It may be that the diagonal position of the leaves in the bud causes pressure at that particular lateral part near the tip of the primary, causing more or less atrophy of that part of the blade. This tendency once inaugurated the rest is simple, for those portions of the leaf at the tips of the primaries would have nearly all their leaf-forming energy expended in increasing the length of the lobe; possibly especially good environment was a factor in the original lobation, as witness the great development of the lateral portions of the leaf blade in the five-lobed forms occurring in rich soil. The Potomac species under discussion bears some resemblance to certain species referred to *Sterculia*, as well as to the asymmetrical terminal leaflets of some compound leaves, but I feel that we are justified in considering it a true *Sassafras*—the first that we can identify as such with any degree of certainty. As pointed out by Fontaine in the fragment of this leaf figured (by him), the opposite primary is considerably stouter than its fellow which runs to the lobe which is preserved, lending color to the supposition that this species was also trilobed.

The next forms which we have to consider are those recorded from the Cheyenne sandstone of Kansas. They were probably contemporaneous with the foregoing or possibly somewhat more recent, and flourished about 1000 miles to the westward.

SASSAFRAS sp. Knowlton in Hill, Am. Jour. Sci. 1: 212. 1895, represents fragmentary remains of doubtful identity from Belvidere, Kansas.

SASSAFRAS OBTUSUM Lesq., first described by him as *Populites salisburyaeifolia* in 1868, then as *Sassafras*, and then as *Cissites*, and SASSAFRAS CRETACEUM OBTUSUM Lesq. had both better be referred to *Cissites*; at least this is a more natural place for them among the Lauraceae. Newberry includes them both in his composite species *S. cretaceum*. They resemble somewhat the trilobate forms of *Cissites harkerianus* Lesq., and also *C. insignis* Heer, and there is a distant resemblance to Dawson's *Sassafras Selwynii* from the Canadian Upper Laramie. They are both found in the Dakota formation, and *S. cretaceum obtusum*

also occurs in the sandstone at Belvidere, Kansas. The primaries are sub-basal, and the secondaries are straighter than in the modern *Sassafras*. The texture of these leaves differs widely, and the basal midrib is very wide. Some specimens show a tendency to become dentate. Hollick¹⁴ compares his *Cissites platanoidea* with *S. obtusum* Lesq.

SASSAFRAS MUDGEI Lesq.—According to Newberry, this is merely a variety of his *S. cretaceum*, but we fail to see any ground for this association except that they resemble somewhat the narrower lobed leaves ascribed to that species. They are somewhat intermediate between these forms and the more typical *S. acutilobum*, but are much more like the modern leaf than either. Lesquereux's *figs. 3* and *4. pl. 14*, Cret. Fl., we consider to be typical forms of this species. In the lengthening of the terminal lobe they approach the modern *Sassafras*; and we see no venation characters which are unlike the modern leaf, for while no marginal veins are discernible, they might have been present in *fig. 3*, and both figures approach *Sassafras* in the relations of their secondary members in this region. If it be certain that the fruit has been found in the same strata as Lesquereux asserts,¹⁵ it only serves to substantiate the impression otherwise obtained that they are true *Sassafras* leaves. The lateral margins of both the base and the lobes are straighter and more ascending than in the existing *Sassafras*, and the margin shows a tendency to become wavy. Lesquereux's other figure referred to this species differs in the size and direction of the lateral lobes, in the sub-basal primaries, and in the acute tip; the venation also is somewhat dissimilar, the ascending margins bulge outward, and the base is not decurrent on the petiole, as it is most markedly in his *figs. 3* and *4*. It resembles somewhat the forms which Newberry refers to *S. acutilobum*, but we do not consider it a *Sassafras*. Ward's fragmentary leaves from the Black Hills are of doubtful identity. The more perfect specimen which he originally referred to *Lindera venusta* Lesq., which it resembles in outline, is a smaller leaf than *S. Mudgei*, with sub-basal primaries, considerable breadth of blade, and

¹⁴Bull. Torr. Bot. Club 22: 226. 1895.

¹⁵Fl. Dak. Group, p. 230.

reduced terminal lobe. It may be Platanoid, Cissoid, or Aralioid, but is hardly a *Sassafras* leaf. If the reference of leaves from the Cheyenne sandstone to this species be correct, it had a considerable range in time, extending from the Lower into the Upper Cretaceous.

SASSAFRAS CRETACEUM RECURVATUM Newb.—Three to five-lobed subcoriaceous leaves; primaries branching from the midrib in the decurrent base, borders undulate; resembling the *Araliaceae* in the tendency to become five-lobed. Newberry's and Lesquereux's figures¹⁶ agree with each other and differ from those of *S. cretaceum*, of which Newberry considers them a variety in the craspedodrome venation, and the tendency of the lobes to become sub-lobate or undulatory, a tendency quite pronounced in Lesquereux's specimens cited. Lesquereux's third figure¹⁷ differs in being distinctly trilobate with camptodrome venation, and greatly resembles in outline the leaves which he refers to *S. cretaceum*. It also resembles his *S. mirabile*, being, however, fuller in its basal half. The typical forms of this species¹⁸ are closely related to some of the forms of *Platanus latior* and *P. Heerii* in the undulate margins and the strong development of the secondary branches from the midrib¹⁹ and undoubtedly should be referred to *Platanus*.

SASSAFRAS LECONTEANUM Lesq.—This name embraces leaves from the Dakota Group at Fort Harker, and remains doubtfully ascribed to Nanaimo, Vancouver island. Schimper²⁰ says of them, "Lauraceae, but doubtful *Sassafras*." Lesquereux²¹ says their "relation is with the European Tertiary Benzoin, and the existing *Nectandra* and *Lindera*." While modern opinion places them in the genus *Persea*, I am disposed to follow Heer in considering them a species of *Magnolia*; they are certainly not *Sassafras*.

SASSAFRAS ACUTILOBUM Lesq.—The leaves from the Amboy

¹⁶ Cret. Fl. pl. 10. figs. 4-5. ¹⁷ Cret. Fl. pl. 10. fig. 3.

¹⁸ NEWBERRY, Later Ext. Fl. N. A., pl. 9, fig. 2, and Lesquereux, Cret. Fl. pl. 10. figs. 4-5.

¹⁹ Compare with Cret. Fl. pl. 7. fig. 2; pl. 8. fig. 4; pl. 9. fig. 1.

²⁰ Pal. Veg. 2: 836.

²¹ Cret. Fl. p. 75.

clays of New Jersey, which Newberry refers to *S. acutilobum*, as well as the single leaf described under this name by Hollick from Glen Cove, L. I., are quite different from the majority of Lesquereux's figured specimens from the Dakota formation, and evidently are not Sassafras leaves. Newberry's two small figures are fragments which resemble *Ficus Woolsoni* in the position and direction of their primaries, the less fragmentary specimens resemble somewhat those leaves which Newberry refers to *Cissites formosus*. They are broad leaves with more or less laterally directed, short, broad, acute lobes; the primaries are all basal except in one specimen which might be a fragment of Sassafras or almost any other triple-veined leaf; the secondaries branch from the midrib at irregular intervals and arch, forming laterally directed loops a considerable distance from the margin. Lesquereux's *S. acutilobum*, on the other hand, has long, narrowly pointed lobes, the primaries are not basal, the secondaries are numerous and branch from the midrib at regular intervals, and ascend in regular curves to join the one next above near the margin. His larger leaf greatly resembles the trilobed leaves which he refers to *Aralia Wellingtoniana* from the same formation.²² The form and size are the same, the primary venation is similar, the secondaries arch with almost the same regularity, and form similar ascending curves. In the *Aralia* leaves, however, the secondaries in the terminal portions are craspedodrome or straight, running to the dentate points of the margin, and the basal portion of the leaf is produced farther down the petiole. It is also very similar to some of Newberry's figures of *S. cretaceum*, and together with them probably represent transition forms between *S. cretaceum* and *Aralia* (so-called). Probable Sassafras fruit has been found in the same strata with *S. acutilobum*²³, tending to show that it is a true Sassafras, notwithstanding its dissimilarities; however, this is not certain, as the leaves and fruit were not found associated. Lesquereux's smallest figure of *S. acutilobum* is considerably smaller, with the lobes directed upward, and is probably a young leaf of his larger form. His other figure approaches some of the leaves which Newberry refers to this species, but has

²² See Fl. Dak. Group, *pl. 21. fig. 1.*²³ LESQUEREUX, Fl. Dak. Group, p. 230.

narrower and more produced lobes; the secondaries, while indistinct, seem to conform to those of Lesquereux's other specimens, thereby differing from Newberry's leaves. The two series are, furthermore, widely separated geographically and are from different geological horizons. As previously stated, the Amboy clay leaves show no affinity to Sassafras; especially is this so in the very small, probably young leaves. Whether the Dakota group forms are Sassafras or not is not easy to decide. No modern Sassafras leaves which I have seen have the primaries and the lateral lobes so nearly horizontal; the secondaries are not so uniformly regular, nor do they curve upward to join the next above at a point. In the modern leaf an outwardly and downwardly directed branch from the latter is emphasized. There is never such an open sinus, amounting as it does to nearly 90° , and the lobes in the modern leaf have their margins inflated and not straight. In these ancient leaves the sinus never has a marginal vein, the secondary in this region forking and striding it, or curving to join its neighbor. In all cases the secondary system seems to be uniform throughout the leaf, while in the modern leaf there is always evidence of changed conditions in that region around the sinus; the secondaries or their representatives from both the primaries and midrib are changed in size and direction and usually belong to the tertiary system. None of the Dakota leaves of this species show the characteristic basal venation of the modern leaf. While we should not, necessarily, expect Cretaceous species to conform to the modern type, still the character of the secondary system in the former is so different from what would obtain in a leaf descended from a simple ancestor, such as we hold Sassafras to have done, that we are inclined to associate these leaves with those trilobed forms which have been referred to *Aralia*, laying aside, for the present, any consideration as to whether or no they are true species of *Aralia*. Lesquereux originally considered his leaves to be a variety of *S. Mudgei*, which form they resemble somewhat distantly. Leaves which have been referred to this species (*S. acutilobum*) have been found in both the Lower and Upper Cretaceous, and at the following localities: Woodbridge and Cliffwood, N. J.; near Ft.

Harker and along the Salina river, Kansas; Glen Cove, Long Island, and at Martha's vineyard. Velenovsky identifies it in the Cenomanian of Bohemia, and Oswald Heer's Greenland specimen which he refers to *S. recurvata* probably belongs here (Fl. Foss. Arct. 6: pl. 39. fig. 4).

SASSAFRAS SUBINTEGRIFOLIUM Lesq.—This leaf Lesquereux refers²⁴ doubtfully to this species. He is positive that it is referable to some member of the Lauraceae, comparing the secondary venation to that of *S. Aesculapi* Heer, and the nearly round or polygonal reticulation to that of Benzoin. Later²⁵ he believed that it represents only a deformation of *S. cretaceum*, especially the var. *obtusum*. The bilobate form is included by Newberry in his *S. cretaceum*, and Lesquereux seems inclined to agree with this reference. Their two figures of bilobate leaves, however, are very dissimilar. The tertiary system and general outline are clearly like Sassafras, the secondaries are more ascending, causing the sinus to be midway between the primary and the first secondary, instead of the secondary running to it and becoming marginal as occurs in the majority of modern leaves; the primary to the entire side is straighter; the lateral branches of the primaries are longer and straighter than in the modern leaf; the pair of secondaries below the primaries is also a character not found in modern leaves, where the lowest lateral branches from the primaries and joins the marginal veins to form an inverted triangle. Passing over the ambiguous form whose positive relations are obscure, we would say in regard to the bilobate form that, while it lacks the basal nervation and the secondary to the sinus of the modern leaf, it is similar in outline, in primary and tertiary venation, and more nearly resembles Sassafras than any other leaf-form. We would therefore retain it in this genus, keeping it separate from the *S. cretaceum* of Newberry.

The Laramie species comprise three or four forms. The first, SASSAFRAS sp. Lesq., from six miles above Spring cañon, Montana, is not afterward mentioned by that author, and as it was never figured we can dismiss it as an undeterminable fragment. We mention also Dawson's SASSAFRAS sp., from the

²⁴Cret. Fl. pl. 3. fig. 5.

²⁵Cret. and Tert. Fl.

Upper Cretaceous of Baynes sound, Vancouver island. All are imperfect specimens, representing a small apparently trilobed leaf of doubtful affinities.

SASSAFRAS SELWYNII Dawson.—Dawson says of this leaf "As much entitled to be referred to *Sassafras* as many of the Cretaceous species; near to *S. cretaceum* Newberry, particularly the variety *obtusum* Lesq." From the Upper Laramie of the Souris river region; it was the first representative of this genus in the Laramie. It resembles *Aralia acerifolia* and *A. notata* Lesq., especially the latter, in its venation. The rounded base and basal primaries preclude us from considering it a species of *Sassafras*.

SASSAFRAS (ARALIOPSIS) BURPEANA Dawson.—From the Canadian Upper Laramie at Shagnappi point, Calgary, Canada. This species can also hardly be considered a *Sassafras*. The secondaries are regularly spaced and straight, the margins of the terminal and one lateral lobe are straight. It may represent the terminal portion of a compound leaf, such as *Rhus* or *Sapindus*²⁶ or it may be the fragment of an *Aralia* leaf (see *A. Masoni* Lesq). Lester F. Ward considers²⁷ both *S. Burpeana* and *S. Selwynii* as belonging to the Platanoid group of leaves. Neither form can be allied to any modern *Sassafras* leaf by any characters they present, unless it be the fact that they are trilobed, as are also some forms of *Aralia*, *Cissites*, *Platanus*, *Aspidiophyllum*, *Menispermities*, etc. This leaves not a single species of this genus in the Laramie, although *Sassafras* must have been present in the flora of that period.

SASSAFRAS (ARALIOPSIS) HARKERIANUM Lesq.—Lesquereux says of this form, "evidently related to *S. cretaceum obtusum* and to *S. obtusum*," and "evidently related to *Araliopsis*." The name includes rounded, trilobate leaves; nearly simple rounded leaves; and simple acuminate leaves very similar to *Cissites acuminatus* Lesq. The primaries are sub-basal as in the latter, or are inserted some distance from the base of the blade as in *Cissites Heerii* Lesq. The trilobate forms are included by New-

²⁶ Compare with Lesq., Fl. Dak. Group, pl. 56. fig. 4; pl. 64. fig. 18.

²⁷ Geol. Dist. Fossil plants, p. 842.

berry in his *S. cretaceum*; his figure however differs from Lesquereux's in that the primaries are as in the modern *Sassafras* and not sub-basal, as in the leaf figured by Lesquereux. It is well to consider these leaves as belonging to the Cissoid group. The veins, both primary and secondary, are straighter than in *Sassafras*, and more ascending, and are usually craspedodrome and not camptodrome as in *Sassafras*. All are found in Dakota strata.

SASSAFRAS PROGENITOR Newberry.—Newberry is very positive that this leaf is a true *Sassafras*, with which view we entirely agree. The small leaf is the exact counterpart of the modern *Sassafras* leaf in outline and venation, with the exception that the primaries are basal. While no marginal veins are visible at the sinuses, the first secondaries leave the midrib and curve upward, running directly to the sinuses as in the existing *Sassafras* leaves. Hollick's specimen from Long island, while fragmentary, has a short branch running to the sinus in the half of the leaf blade which is preserved. Newberry's other figures each lack the basal portion of the blade and one of the lateral lobes; the lobes are more obtuse than in his smaller specimen. While the sinus appears to lack a marginal vein, the disposition of the secondaries and tertiaries in this region is *Sassafras*-like. The species is thus far confined to the Potomac formation, extending from the Amboy clays to the Island series, and is remarkable in that a Lower Cretaceous form should resemble so closely the existing species.

SASSAFRAS DISSECTUM Lesq.—These very large, palmately five-lobed, coriaceous leaves from the Dakota formation of Kansas were hardly borne upon a *Sassafras* tree. They resemble somewhat *S. mirabile* and *Platanus primaeva*, and Lesquereux considers them²⁸ a possible link between these two genera. Later he compares them to *Aspidiophyllum trilobatum*, from which they differ in their entire lateral lobes; in the smooth and not rugose areolation; and in having a narrow decurrent, instead of an expanded base. Aside from the character of the

²⁸ Fl. Dak. Group, p. 101.

base, they also resemble Lesquereux's figure²⁹ of *Aspidiophyllum dentatum*, agreeing exactly except that in the latter the border is sometimes obtusely dentate.

SASSAFRAS DISSECTUM SYMMETRICUM Hollick.—What was said of *S. dissectum* applies equally well to this variety, at least in so far as its characters are known. The fact that the primaries are opposite is hardly a varietal character, as witness the variability in this respect among leaves of the existing Sassafras. The only other differential character, therefore, is that the leaf-blade is not decurrent on the petiole but ends at the insertion of the primaries. As the general shape of the base is like that of the species, and as the variety is founded on a single imperfect specimen, it would perhaps be well to consider it as identical with *S. dissectum*, at least until the discovery of more complete material. The specimen in question is from the Dakota formation near Fort Harker, Kansas.

SASSAFRAS CRETACEUM Newberry.—Newberry includes under this name the various forms described by Lesquereux as *S. Mudgei*, *S. subintegrifolium*, *S. integrifolium*, *S. obtusum*, *S. cretaceum dentatum*, *S. cretaceum obtusum*, *S. acutilobum*, *Cissites harkerianus*, and *C. salisburiaefolius*. While this shows the undoubted composite nature of *S. cretaceum*, it also shows that the extremes of leaf form above mentioned are so closely connected with the more typical leaf by a series of intermediate forms that the question of where one species shall end and another begin is an extremely difficult one. We consider the leaf figured on *pl. 6. fig. 1*, Later Ext. Fl., to be the typical form of this species. It bears considerable resemblance to some modern Sassafras leaves. A slight widening of the terminal lobe of some of these in the region of its base would give a leaf strikingly like *S. cretaceum*; or were the sinuses of the latter slightly deeper we would have the typical modern leaf. The basal portion of the leaf is like Sassafras, and the indications point to a similar venation in this region. The first pair of secondaries do not branch to form margins of the sinuses; the left one runs directly to the sinus, however, and may possibly have con-

²⁹ Fl. Dak. Group, *pl. 39. fig. 1*.

formed to the margin, but so small as to have been effaced in the specimen; the right one is stronger and runs almost to the sinus where it makes a sharp turn upward, continuing until it joins the next secondary. This feature is analogous to those in the modern leaf, which indicates the mode of origin of this peculiar character. This leaf seems to form a central figure from which a series of forms grade in several directions, culminating in quite dissimilar leaves. Lesquereux's *S. cretaceum* is a more Platanoid leaf, with more acute tips, a tendency to become dentate, and with the primaries inserted nearer the base. Closely allied to the preceding is his *S. (Araliopsis) mirabile*, which serves as a connecting link with his *Platanus recurvata*. From the aforementioned *S. cretaceum* of Lesquereux it is but a step to such a leaf as the one shown on *pl. 8. fig. 2*, Later Ext. Fl., and to the trilobed forms referred to *Cissites harkerianus*, and these in turn grade into the more Cissoid forms of this species, such as those shown on *pl. 11. fig. 3*, Cret. Fl. The primaries are basal and of not much greater caliber than the regularly succeeding straight secondaries. It is but a step from this leaf to that of *Cissites Heerii* on the one hand, with its palmately five-pointed blade; and to such forms of *Cissites acuminatus* as *pl. 5. fig. 4*, Cret. and Tert. Fl. on the other; which in turn, by the elimination of the decreasing dentate points, gives us the leaf figured at *3, pl. 5*, Cret. and Tert. Fl. In the second series of leaves diverging from the typical, *S. cretaceum*, *pl. 8. fig. 1*, Later Ext. Fl., is removed a slight distance by the shortening of the blade, the thickening of the primaries and secondaries, and the shortening and rounding of the lobes (*S. obtusum*); while a smaller leaf would be its logical descendant; and from these leaves to those referred to the typical *Cissites salisburiae-folius* is but a step. In the third series of leaves diverging from the typical *S. cretaceum*, we note that the leaf has its lobes much produced, narrow and running to a sharp point, as in the beautiful leaf on *pl. 7. fig. 1*, Later Ext. Fl., which however is still referred to *S. cretaceum*. Lesquereux's *S. acutilobum* does not differ from the preceding except in the direction of the lobes, which is scarcely a specific character. From this leaf it is no

great jump to those trilobed forms which are referred to *Aralia Wellingtoniana*, the chief difference being in the margin. Thus we have an interrelated series connecting those leaves which undoubtedly show affinity to *Sassafras* with those which are undoubtedly Platanoid on the one hand, and with others which are reasonably referred to *Cissites* and *Aralia* on the other.

SASSAFRAS MIRABILE Lesq.—Lesquereux says³⁰ of this leaf "its facies is like that of a *Platanus*, or of a group referable, perhaps, to the *Araliaceae*, like *Platanus nobilis* Newb., *P. jatropaefolia*, and *P. hercules* Unger, etc." Its size, texture, obtusely dentate borders, and craspedodrome secondaries all stamp it as a *Platanus*, and we prefer to follow Newberry and consider it as variety of his *P. latiloba*. There is a distant resemblance to the trilobed forms of *Cissites harkerianus*, as well as to some forms which have been referred to *Sassafras cretaceum*; this however, is a much larger leaf than the latter, with sub-basal primaries.

SASSAFRAS (ARALIOPSIS) PAPILLOSUM Lesq.—Lesquereux writes of this leaf "though the general aspect of the fragment is like that of a leaf of *Platanus*, it has a more evident relation to *Sassafras (Araliopsis) mirabile* Lesq., from which it differs merely by the enlarged lateral lobes, the acutely dentate borders, and the papillose teeth; this has a marked degree of affinity to *Platanus primaeva* Lesq. and its varieties." It is very similar to some of the leaves referred to *S. cretaceum*, especially the var. *grossedentatum* Lesq., and like the latter its more natural position is with the leaves of the Platanoid group, resembling as it does *P. latior*, *P. dissecta*, *P. latior grandidentata*, etc.

SASSAFRAS (ARALIOPSIS) PLATANOIDES Lesq.—It is not difficult to find analogues of this leaf in widely different genera. There are three forms from the Lower Potomac which it resembles: *Araliaephyllum acutilobum* Font., *Araliaephyllum aceroides* Font., and *Aceriphyllum aralioides* Font. Lesquereux³¹ considers it to be closely related to *Platanus Heerii*, but I fail to detect the resemblance in his published figures. Nearly all the five-lobed modern leaves of *Sassafras* resemble this species (*S. platanoides*)

³⁰ Cret. Fl. p. 81.

³¹ Cret. and Tert. Fl., p. 58.

in outline, the chief difference being that the main lateral sinuses are deeper in the modern leaf, thus giving the lobes somewhat orbicular outlines. The position of the primaries is similar; the branch from the primary to the extra lobes is similar; the secondaries are somewhat straighter in the ancient leaf. Although Lesquereux says "it is equally referable to *Sassafras* or to *Platanus*," we are disposed to consider the former as representing its more natural disposition, not only because of its similarity to the modern leaves just pointed out, but also in its narrowly produced base, and especially in the first secondary running direct to the sinus, as it seems to do in Lesquereux's figure; for although a small portion of this part of the leaf is missing, it is so nearly complete on the one side as to leave no alternative ending for the secondary in question.

SASSAFRAS (?) PRIMORDIALE Lesq.—This fragment from the Dakota group is of doubtful value. Its only distinguishable characters, namely the basal lobe with the narrowly extended terminal lobe and the secondary in the region of the sinus widely forked, certainly do not warrant its association with *Sassafras*. Lesquereux notes its resemblance to *S. acutilobum* and *S. Mudgei*.

SASSAFRAS CRETACEUM GROSSEDENTATUM Lesq.—Lesquereux says of this form that it "differs in nothing from the normal form except by its large size, with its borders deeply dentate. It is evident that the sharply acute teeth constitute a variety indicated already by the short teeth sometimes seen in the normal forms of the species." In all the leaves referred to *S. cretaceum*, however, the base is decurrent on the petiole as in the modern *Sassafras* leaf. Furthermore, in all of Newberry's figures of the species, while the margins are sometimes slightly toothed, the secondaries remain camptodrome and do not enter the teeth, thus differing from the leaf under consideration as well as from Lesquereux's figures of *S. cretaceum*,³² in which the secondaries are craspedodrome; the base, however, is decurrent as in Newberry's figures and in the modern leaf. This form differs but slightly from *S. papillosum*, and also bears considerable resem-

³² Cret. Fl., pl. 11. figs. 1-2.

blance to some of Lesquereux's figures of *Platanus latior* and some of its varieties, as well as to other species of *Platanus*; and there is no doubt in my mind of its Platanoid affinities.

SASSAFRAS HASTATUM, Newb.—Trilobed, hastate leaves with conical lobes, the lateral ones directed horizontally except in two specimens which approach somewhat *S. progenitor* from the same formation, especially Newberry's fig. 5, pl. 27, Fl. Amboy Cl., which in all probability should be referred to that species. The rest of his figures show the normal form of *S. hastatum*, which differs widely from any leaves which can with any degree of certainty be referred to *Sassafras*; they resemble somewhat the fragments referred by Newberry to *S. acutilobum*. In these, although the lateral lobes are horizontal, they are not basal, and in consequence the primaries branch from the midrib at an angle of about 30° instead of nearly 90° , as in *S. hastatum*. They also resemble the Amboy clay leaves referred by Newberry to *Aralia groenlandica*; and they also have somewhat the appearance of *A. polymorpha*, but differ in outline. The secondary system is more or less obscured, the primaries are horizontal as are the lateral lobes; all the lobes are conical; and the base is not decurrent on the petiole. No discernible characters hint at any *Sassafras* affinities; and the outline is so far removed from what obtains in any forms of the modern leaf that we are inclined to discredit their reference to that genus.

Of the two remaining forms which have been referred to this genus, SASSAFRAS (ARALIOPSIS) sp. Lesq. from the Amboy clays of Burts creek, N. J., is of doubtful value; and SASSAFRAS (ARALIOPSIS) CRETACEUM DENTATUM Lesq., representing obscurely dentate leaves of somewhat doubtful affinity, which serve to connect his *S. cretaceum* with its variety *grossedentatum*, both of which varieties seem more nearly related to *Platanus* than to *Sassafras*.

The varying similarity and interrelation of the forms heretofore referred to *Sassafras*, *Aralia*, *Platanus*, *Aspidiophyllum*, *Cissites*, etc., clearly indicate that a change must soon be made in our conception of these genera; and this not only applies to *Sassafras*, but to the various forms referred to the other genera as well, including also *Grewiopsis*, *Menispermites*, *Credneria*, etc.

Ward suggested³³ that they be referred to a new genus to be designated *Protoplatanus*, or some similar name indicative of their ancestral character; but it seems to me that such a comprehensive genus would be an unwieldy composite no more satisfactory than the present state of affairs, for surely *Platanus* was not the only modern form with this style of a leaf that has Cretaceous ancestors. Other Spermatophytes are well represented in strata of corresponding age, and analogy leads us to see no reason why *Sassafras*, *Aralia*, *Cissus*, *Liquidambar*, etc., should not be present. We may reasonably expect that the more we know of this flora the more it will be found to resemble the existing flora of North America; in fact, the tendency of paleobotanists has always been to underestimate the age of the American Cretaceous. All, or the majority of the Spermatophytes originally had, in all probability, simple leaves; their origin was polyphyletic; and it is very possible that a like environment caused lobation which was thus more or less similar in all of these genera, although the species were quite different in other respects. At the present day a series of leaves of *Vitis*, *Ampelopsis*, *Viburnum*, *Acer*, *Platanus*, etc., could be obtained which would appear to be as closely interrelated as are some of the Cretaceous forms.

SUMMARY.

Of the twenty-eight American forms which have been referred to *Sassafras* the following disposition is made:

Retained in *Sassafras*: *S. bilobatum*, from the Potomac formation; *S. Mudgei*, from the Cheyenne and Dakota sandstones; *S. progenitor*, from the Raritan and Island series; *S. subintegrifolium*, *S. platanoides*, and *S. cretaceum* (in part), all from the Dakota formation.

Referred to *Aralia*: *Sassafras acutilobum*, doubtfully.

Referred to *Cissites*: *S. harkerianum*, *S. obtusum*, and *S. cretaceum obtusum*.

Referred to *Platanus* or *Protoplatanus*: *S. dissectum*, *S. dissectum symmetricum*, *S. mirabile*, *S. papillosum*, *S. cretaceum dentatum* and *grossedentatum*, and *S. recurvatum*.

³³ Bull. 37, U. S. Geol. Surv.

Doubtful: *S. parvifolium*, *S. cretaceum heterolobum*, *S. sp.* Lesq. (from Montana), *S. sp.* Dawson (from Canada), *S. sp.* Knowlton (from Kansas), *S. sp.* Lesq. (from New Jersey), *S. Selwynii*, *S. Burpeana*, *S. Leconteanum*, *S. primordiale*, and *S. hastatum*.

PASSAIC, N. J.

EXPLANATION OF PLATE XVIII.—One-half contours of leaves of *Sassafras Sassafras*, showing variety of lobation; reduced three-fourths.



BERRY on SASSAFRAS

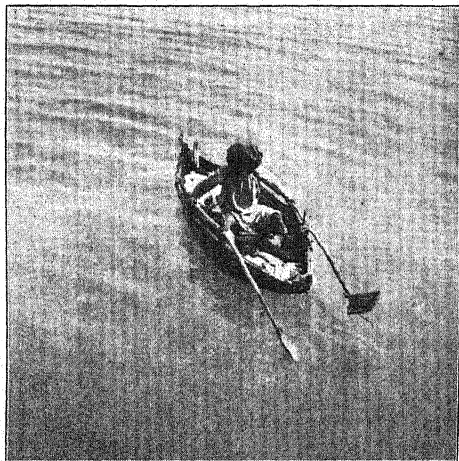


BRIEFER ARTICLES.

A DATE-LEAF BOAT OF ARABIA.

(WITH THREE TEXT FIGURES)

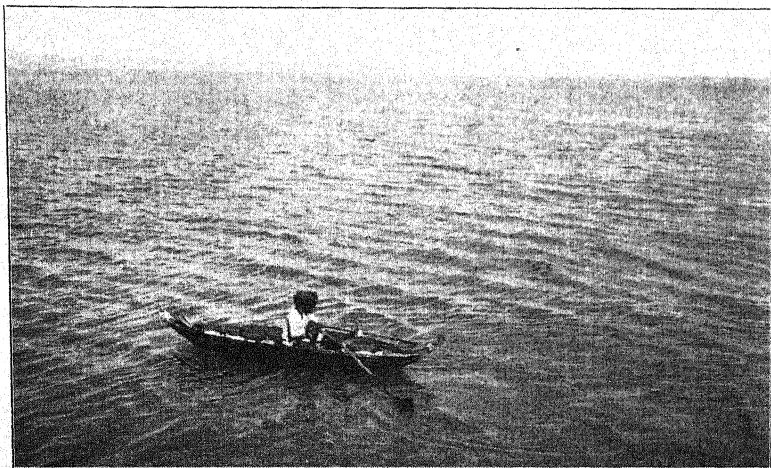
WHILE traveling up the coast of Arabia last February the writer's attention was attracted to some curious craft made entirely of date leaves that came alongside as the "Pemba" steamed into the desert harbor of Jask on the Arabian coast. The coast of the Persian gulf is so barren that one can travel for many days along it without finding so much as a single tree or shrub, and at this place the only plants of any size were some groves of date palms and a few acacias which had been planted by the English employees of the Persian gulf cable company, which has a station at Jask.



Wood is so scarce in the region that even the roots of such small desert shrubs as are to be found are dug up for fuel, and timber large enough for boat building would have to be brought by water from Bombay. It is necessity, therefore, which has invented these curious date boats of Jask. They are made of the midribs of the date palm leaves, which are about an inch and a half in diameter and ten feet long. These tough midribs, from which the leaflets have been removed, are fastened together by means of wooden pegs and strong twine in the form of a boat. No attempt is made to match joints, but a false bottom is built to the craft, and the mass of light midribs that lie beneath this bottom buoy the boat up out of the water so that the inside remains quite dry.

Though in the form of a boat, this curious date-leaf affair is really a boat-shaped raft, for nothing but the fact that the bottom stands high out of the water prevents the waves from entering and flooding it.

They are not pitched or painted in any way, and would doubtless



be short-lived were they not dried out carefully on the beach whenever the owner is not using them. The paddles are the only parts of the boat which are not made of the date palm, being crooked, irregular



poles with the sides of some dry goods box for blades. They indicate the remarkable dearth of wood in the region.

They are weird little craft, and add one more use to the list of things which can be made from this remarkable desert palm.—DAVID G. FAIRCHILD, *Agricultural Explorer, U. S. Department of Agriculture.*

A VARIABLE LARKSPUR.

THE genus *Delphinium*, both in the Rocky mountains and in California, runs into numerous local races or species. Formerly these were classified under a few specific names, but this method had the unfortunate result of grouping together without distinction very diverse plants. Now we are going to the opposite extreme, and the list of species is becoming very long. In all probability we shall eventually come to regard the majority of the distinguishable forms as subspecies or races only; but for the present the chief aim is to separate the different plants, whether or not we can reach final conclusions regarding their status. Whatever the nomenclatural outcome, there will evidently be much to interest the student of evolution.

In the Sapello cañon, Las Vegas range, New Mexico, a peculiar and variable *Delphinium* is very abundant. The writer in 1900 described it as a new species, but the description was not immediately published, and presently many new species were recorded from Colorado and elsewhere, so that the subject became complicated. The plant was clearly related to *D. occidentale*, and it seemed possible that it might be a southern form of *D. multiflorum* Rydberg 1902. I sent specimens representing the variations to Professor Aven Nelson, who has an intimate field knowledge of the Rocky mountain larkspurs, and he fails to recognize the plant, remarking that it is "certainly a fine species." He also agrees with me that the specimens sent are all of one species. Under these circumstances it seems desirable to publish a description.

***Delphinium sapellonis*, n. sp.**—Strict, up to six feet high: leaves tripartite, the lateral divisions large, and themselves almost tripartite: flowers very dull-colored: spurs obliquely ascending, slightly curved downwards, dark purple above, green below, varying to all pale with a dark purple line above: sepals brownish or greenish-white, veined with purple: anthers with an indigo-blue longitudinal band: lower petals purple, with their apical lobes pale, with light yellow hairs: pods with a short but rather dense glandular pubescence: upper part

of stem densely glandular-pubescent: flowers more or less glandular-pubescent.—Beulah, Sapello cañon, described from life, Aug. 11, 1900. The following are variations:

(a) Lower, about three feet high; *heads in bud erect*; truncate; *buds pale green*, nodding, the uppermost transverse; spur about 9^{mm} long, rather slender and pointed; *linear bracts never reaching beyond middle of bud*, in most flowers shorter than peduncles; lower part of stem glabrous, with a whitish bloom, upper part and inflorescence glandular-pubescent.—Beulah, July 27. 1902.

(b) Tall; *heads in bud nodding*, tapering; *buds, including spur, very dark purplish*; spur obliquely truncate; *linear bracts far surpassing buds*.—Beulah, July 27.

(c) *Heads in bud erect*; *buds dark purple*; spur rounded, broad and thick; *linear bracts not surpassing buds*, little longer than peduncles.—Beulah, July 29.

These apparently distinct forms are connected by plenty of intermediates, and often grow together.

A specimen of *D. sapellonis* has been placed in the U. S. National Museum.—T. D. A. COCKERELL, *East Las Vegas, N. M.*

CURRENT LITERATURE.

MINOR NOTICES.

WITH THE APPEARANCE of the second fascicle² of the second volume, Halácsy's *Flora of Greece* is complete. This last fascicle completes Campanulaceae and closes with Labiatae.—J. M. C.

A SECOND EDITION of Green's *Forestry in Minnesota*² has made its appearance. Part I of the first edition³ has been better classified and extended, and Part II, which deals with the trees of Minnesota, has been brought up to date. The work is certainly deserving of the wide circulation which the first edition has received.—H. N. WHITFORD.

THE SEVENTH VOLUME (2d series) of *Contributions from the Botanical Institute*⁴ of the University of Pavia contains 356 pages of text and twenty lithographic plates. There are twenty-five papers and notes, largely cryptogamic, but also concerning the histology of some higher plants and on physiological subjects. There is also a short biographical sketch and portrait of Giuseppe Moretti.—B. M. DAVIS.

THE FIRST ANNUAL ISSUE for Botany in the International catalogue of scientific literature has appeared, and proves to be only a first part. The literature cited is that of 1901, but the work of the "Regional Bureaus" has not been well organized. In fact, so far as American botanical literature is concerned this part might as well not have been issued. The curious random selection of about 150 American titles, sometimes inaccurately cited, suggests the hit-and-miss work of clerks who had no access to American botanical literature, and no knowledge to enable them to select intelligently from such as they did see. This seems especially inexcusable, since a single volume of the *Bull. Torr. Bot. Club*, with its "Index to American literature," would have secured most of the necessary citations of American literature in convenient form. The organization for botanical citations must be upon some more rational basis before the Catalogue will commend itself to botanists.—J. M. C.

¹ HALÁCSY, E. de, *Conspectus Florae Graecae*. Vol. II. fasc. II. pp. 257-612. Leipzig: Wilhelm Engelmann. 1902. *M* 8.

² GREEN, S. B., *Forestry in Minnesota*, 2d ed., pp. 401, *pls.* 63, *figs.* 47. St. Paul, Minnesota: Pioneer Press Co. 1902. Price 25 cents.

³ BOT. GAZ. 27: 228. 1899.

⁴ Atti dell' Istituto Botanico dell' Università di Pavia. II. 7: 1-356. *pls.* 1-20. 1902.

ROBINSON⁵ has published an account of the flora of the Galapagos islands, being one of the papers from the Hopkins-Stanford expedition. The peculiar character of the vegetation of these islands was brought to scientific attention in 1847 by Sir Joseph Hooker, his material being based chiefly upon the collections of Charles Darwin made on the voyage of the "Beagle." Hooker enumerated 239 species, of which 107 were described as new. In 1852 N. J. Andersson visited the islands, collecting 338 numbers, which being distributed in sets to the leading herbaria have long furnished the chief reference specimens for that peculiar flora. Since that time there has been no general revision of the flora, although the islands have been visited and plants collected on them. The occasion of the present contribution is the recent collection secured by the Hopkins-Stanford expedition, and referred to the Gray Herbarium by the Zoological Department of Stanford University.

The flora of the Galapagos islands is almost wholly American in character, but it is impossible to trace its relationship closely to any one section of the Pacific American vegetation. The xerophytic elements show a considerable resemblance to the desert flora of southern Peru and the drier parts of the Andes; while the mesophytes correspond most nearly to plants of Ecuador, Colombia, Central America, and southern Mexico. The composition of the flora is peculiar in the absence of certain great groups. There are no gymnosperms, palms, aroids, rushes, Liliaceae; in fact, outside of grasses and sedges the monocotyledons are represented by some half dozen scattered species. Such characteristic tropical American dicotyledonous families as Sapindaceae, Myrtaceae, Melastomaceae, Lythraceae, and Onagraceae are scarcely or not at all represented; while the best represented dicotyledonous families are Amarantaceae, Nyctaginaceae, Aizoaceae, Leguminosae (about 10 per cent of the spermatophytic vegetation), Euphorbiaceae (about 12 per cent), Malvaceae, Cactaceae, Convolvulaceae, Boraginaceae, Verbenaceae, Labiatae, Solanaceae, Rubiaceae, and Compositae (about 13.5 per cent). The statistics show 54 species of pteridophytes and 445 species of spermatophytes; of the former there are only 3 endemic species, of the latter 236, that is, nearly 45 per cent. of the spermatophytic flora. Of the 239 endemic vascular plants, 130 are restricted to a single island.

About 30 new species are described, distributed among the following genera: Chloris, Peperomia, Pilea, Phoradendron, Froelichia, Telanthera (3), Mollugo, Bursera, Acalypha (3), Euphorbia, Cereus (2), Opuntia, Miconia, Hydrocotyle, Acnistus, Justicia, Acanthospermum, and Scalesia (5). A new species of Glossophora, and a new genus (*Herpophyllon*) of Rhodophyceae are described by Dr. Farlow.—J. M. C.

⁵ ROBINSON, B. L., Flora of the Galapagos islands. Proc. Am. Acad. 38: 77-269. pls. 1-3. 1902.

NOTES FOR STUDENTS.

THE THIRTEENTH PART (Jour. Linn. Soc. 26: 538-561. 1902) of Forbes and Hemsley's "Enumeration of all the plants known from China proper, Formosa, Hainan, Corea, the Luchu archipelago, and the Islands of Hong-kong" contains the gymnosperms of that very interesting region, the enumeration being as follows: Gnetales 5 spp. (Ephedra 4, Gnetum 1); Coniferales 64 spp. (Libocedrus 1, Thuja 1, Cupressus 2, Juniperus 7, Cryptomeria 1, Glyptostrobus 1, Cephalotaxus 5, Taxus 1, Torreya 2, Podocarpus 6, Cunninghamia 1, Pinus 11 [1 new], Picea 6, Keteleeria 4 [2 new], Tsuga 4, Abies 4, Pseudolarix 1, Larix 6); Ginkgoales 1 sp.; Cycadales 4 spp. (Cycas). —J. M. C.

THE GERMINATION of dry seeds after exposure to high temperatures has been studied by Dixon.⁶ After being desiccated for a day at 65° to 75°C., and then for another day at 90°C., the seeds were subjected to the various temperatures for one to two hours, and then planted. In seeds which have been subjected to high temperatures germination is much slower than in the control. Also growth of the seedling is often abnormal in the case of heated seeds. The author believes, on experimental grounds, that the retardation of germination is due to some effect of the heat *per se*, and not to more complete desiccation. Some maximum temperatures withstood are the following: *Avena sativa*, 118°; *Cucurbita pepo*, 112°; *Helianthus annuus*, 112°; *Lotus tetragonolobus*, 100°; *Convolvulus tricolor*, 120°. These experiments emphasize again the great importance of imbibed water as a controlling factor in protoplasmic phenomena.—BURTON E. LIVINGSTON.

CULTURES OF PLANT RUSTS, made by Freeman⁷ during the three months from March to June of the present year, are reported in the *Annals of Botany* for September. The work was done under the direction of Professor Marshall Ward at Cambridge University, and is in line with investigations instituted by Professor Ward, and in part already reported. Only uredospores of *Puccinia dispersa* E. and H. were used, obtained from but two hosts, *Bromus mollis* and *B. sterilis*, representing two of the five sections of the genus. These were sown upon forty species and varieties of *Bromus*, of which twenty-two showed no infection. Of the remaining kinds five were infected by spores from both sources, eleven were only infected by spores taken from *B. mollis*, while *B. sterilis* was the only kind out of the forty that could be infected with spores from *B. sterilis* alone. To secure these results about fifteen hundred cultures were made. It is such thorough and accurate work as this that will eventually give us a clear notion of the relationships of our common cereal and meadow rusts.—J. C. ARTHUR.

⁶ DIXON, H. H., On the germination of seeds after exposure to high temperatures. Notes from Bot. School Trinity Coll. Dublin 5: 176-186. 1902.

⁷ FREEMAN, E. M., Experiments on the brown rust of bromes (*Puccinia dispersa*). Ann. Botany 16: 487-494. 1902.

IN HIS DISCUSSION of the phylogeny of the cotyledon, Lyon⁸ concludes that it is a sucking organ of the embryo derived from the so-called foot of bryophytes and pteridophytes. His own summary is as follows: (1) The typical embryos of the pteridophytes and angiosperms differentiate into three primary members—the cotyledon, stem, and root; (2) cotyledons are not arrested leaves but are primarily haustorial organs originating phylogenetically as the nursing-foot in the bryophytes and persisting throughout the higher plants; (3) the monocotyledonous condition is the primitive one and prevails in the bryophytes, pteridophytes, monocotyledons, and some gymnosperms; the two (sometimes more) cotyledons of the dicotyledons are jointly the homologue of the single cotyledon of the monocotyledons; (4) the cotyledon always occurs at the base of the primary stem; (5) the hypocotyl is a structure peculiar to the angiosperms, being differentiated between the primary stem and root; (6) the so-called cotyledons of the pteridophytes and gymnosperms, with the probable exception of Ginkgo and the cycads, are true foliage-leaves.—J. M. C.

ITEMS OF TAXONOMIC INTEREST are as follows: T. E. HAZEN (Mem. Torr. Bot. Club 11: 135-250. *pls.* 20-42. 1902) has published a revision of the Ulothricaceae and Chaetophoraceae of the United States. The species recognized in the former family are 8 in Ulothrix, 7 (1 new) in Stichococcus, 9 (2 new) in Microspora, and 3 in Tribonema; in the later family the species are 2 in Microthamnion, 13 (5 new) in Myxonema, 4 (1 new) in Chaetophora, 4 (1 new) in Draparnaldia, 1 each in Epicladia, Endoderma, and Bolbocoleon, 2 in Chaetosphaeridium, and 1 in Herpoteiron. The 23 colored plates illustrate the species very completely.—L. M. UNDERWOOD and W. R. MAXON (Bull. Torr. Bot. Club 29: 577-584. 1902), in publishing an account of a collection of Cuban pteridophytes, have described new species of Alsophila, Polypodium, Asplenium, and Diplazium.—W. A. MURRILL (*idem* 599-608), in his first paper upon the Polyporaceae of North America, has presented the genus Ganoderma, recognizing 7 species, and describing 5 of them as new.—M. L. FERNALD (Am. Jour. Sci. IV. 14: 167-194. *pls.* 5-6. 1902), in studying the relationships of some American and Old World species of Betula, has united some well-known trees and shrubs of the two hemispheres.—J. M. C.

BREBNER⁹ has published a detailed account of the development of the stem in Danaea. The author takes exception to the morphological terms *phleoeterma* and *siphonostele*, proposed by Strasburger and Jeffrey respectively, on the ground that they imply certain homologies which he is not prepared to accept. As an alternative to these morphological terms, he

⁸LYON, HAROLD L., The phylogeny of the cotyledon. *Postelsia* 1901: 55-86. 1902.

⁹BREBNER, G., On the anatomy of Danaea and other Marattiaceae. *Ann. Botany* 16: 517-552. *pls.* 22-23. *figs.* 28. 1902.

proposes a large number of purely formal descriptive terms, for which the reader is referred to the article in question. According to Brebner, "the haplostele (protosteles of the young stem) does not pass through a medullated stage, but becomes crescentic after the departure of a variable number of leaf traces. When this stage is reached, the next leaf-trace passes off from the convexity of the crescent, thus causing a distinct leaf gap. Two meristeles are left behind with what is usually regarded as extra-stelar tissue between them. The crescent gap is closed, a leaf trace is given off, the gap is closed again, etc. By the repetition of the process, followed by branching, anastomosis, and increase in the number of leaf trace meristeles, at length a network of strands, or the dictyostele, is formed." The course of development appears to follow substantially that described for the Marattiaceae by Farmer, Hill, and Jeffrey. The author states that there is a great deal of uniformity in the anatomy of the Marattiaceae, all being adelosiphonic, with a greater or less tendency to dorsiventrality.—E. C. JEFFREY.

DICTYOSTELIUM MUCOROIDES, one of the Myxomycetes, was discovered and described by Brefeld in 1869, since which time several investigators have studied its morphology and cultural reactions. Nadson, in 1899, asserted that he had obtained it in absolutely pure culture, although he found that it grew better with bacteria, and especially that a symbiosis existed between the mould and *B. fluorescens liquefaciens*. Potts,²⁰ however, has found that *D. mucoroides* will not develop entirely free from bacteria, and that the species which he isolated in connection with it was a new form, named by him *Bact. fimbriatum*. By a series of ingenious experiments he determined that symbiosis did not take place between *D. mucoroides* and either *Bact. fimbriatum*, *B. megatherium*, *B. subtilis*, or *B. fluor. liq.*, i. e., that although the mould derived benefit from the presence of the bacterium, its effect was injurious upon the latter, which underwent extracellular digestion, apparently by an enzyme secreted by the plasmodium. Living bacteria were not necessary to *D. mucoroides*, which could flourish, not upon the metabolic bacterial products, but upon the dead organisms. Besides *D. mucoroides*, a protozoan, *Amoeba nitrophila*, has been found to nourish itself through extracellular digestion (see Frosch, *Zur Frage der Reinzüchtung der Amöben*, Centr. b. Bact. 21²: 1897). It is probable that the same is true of many other Myxomycetes and Protozoa whose method of nourishment has been problematical. The author made no attempt to isolate the enzyme, but carried out detailed experiments to determine the effect of various non-proteid media and of light, temperature, and moisture upon cultures of *D. mucoroides* and *Bact. fimbriatum*. For the germination of spores, oxygen, phosphate, organic substance, and water are necessary. Optimum reaction is 0.1 per cent. to 0.2 per cent. alkaline; optimum tempera-

²⁰ POTTS, GEO., Zur Physiologie des Dictyostelium mucoroides. Flora 91: 281-347. figs. 2. 1902.

ture, 23°–25° C. Attempts to isolate the mould with *B. Anthracis* or a pink yeast resulted negatively.—MARY HEFFERAN.

AN IMPORTANT CONTRIBUTION to the subject of the relation of parasite and host among the plant-rusts has been made by Professor H. Marshall Ward¹¹ in the *Annals of Botany*. The summer (uredo) spores of brown rust were sown upon seedlings of all available species of grasses belonging to the genus *Bromus*. The spores were obtained from *Bromus mollis*, *B. sterilis*, and *B. secalinus*. The result in general was the infection of most species belonging to the section of the genus which included the host from which the spores were taken, and not of species belonging to other sections of the genus.

The author undertook to find out if any anatomical or morphological differences existed in the hosts which might account for the immunity of some hosts and the susceptibility of others to the attack of the rust, and in so doing developed a wealth of data regarding the number of stomata and hairs per given area, the size of stomata, the number of leaf ribs and distances between them, the comparative area of chlorophyll tissue, and many other details that must challenge the admiration of every investigator. Each set of data is compared with the "curve of infection" and the charts so constructed show with great clearness that no correspondence exists. The discussion of these data touches upon many points that can not be mentioned here, but is most lucid and convincing and ends with the statement, that "we are driven to conclude that the factors which govern predisposition on the one hand, and immunity on the other, are similar to those which govern fertility and sterility of stigmas to pollen." It is, therefore, to be referred, so far as we can now judge, to the quality of nutriment afforded by each host, including, doubtless, some less evident factors.

In carrying on the work it was found necessary to institute an investigation into the characters and limitations of the species of *Bromus*, and considerable information regarding the seeds and seedlings especially is given.

Of conditions that inhibit the development of the rust, temperature was found to be the most important, the upper and lower limits being about 27° and 10° C. respectively. The presence of green algae, or the spores of molds and other fungi, had no perceptible effect on the germination of the rust spores, neither did the presence or absence of light.

Although the paper is notable for the breadth and thoroughness of the observations, it is even more important for the clear and far reaching conclusions that are drawn from the data. It will do much to throw light upon an intricate and obscure subject.—J. C. ARTHUR.

DANGEARD¹² has recently published an extensive account of the Euglenineae. The material is very poorly arranged, without index or even a suitable

¹¹ WARD, H. MARSHALL, On the relations between host and parasite in the bromes and their brown rust, *Puccinia dispersa* (Erikss.). *Ann. Botany* 16: 233–315. 1902.

¹² P. A. DANGEARD, Recherches sur les Eugleniens. *Le Botaniste* VIII. fascs. 3–6, 97–370, pls. 4. figs. 53. 1902.

table of contents, and its value is therefore much impaired. Following a rambling introduction, partly historical and partly descriptive of structure and methods, is a description of the genera and species. This account is lengthy and so deficient in keys and synopses as to be of little value to the general student. The second part of the paper contains five chapters devoted to structural details, movements, nutrition, and methods of reproduction. As is well known, the Euglenineae present a wide range of variation in their feeding habits. Only one of three families, the Euglenaceae, have a halophytic nutrition, the other groups entirely lacking chlorophyll. One family, the Peranemaceae, engulfs its food as solid material in an animal-like fashion. Other forms, the Astasiaceae, are saprophytic, preferring water foul with organic matter. The Euglenaceae are especially interesting. Although generally containing chloroplasts, they may under certain conditions adopt saprophytic habits, when the chlorophyll disappears and the cell is quite devoid of pigment. The plastids in such cells are believed to remain as leucoplasts, which regain their green color under proper environment. Some of the species are normally without color.

Euglena gracilis is remarkable for its power of adaptation to food relations. It becomes colorless under saprophytic conditions, as when cultivated in sugar solutions away from light, but it regains its green color very readily if brought back to a more normal environment. There are differences of opinion as to the behavior of the plastids. Former writers have held that the chloroplasts simply lose their color, becoming leucoplasts, which remaining in the cell as organized bodies, assume again the chlorophyll when such was reformed in the organism. Dangeard believes that the chloroplasts may disappear entirely and be formed again *de novo*.

The chief events of nuclear division are as follows: The resting nucleus consists of a nucleolus surrounded by a chromatic spirem which is not clearly divided into segments. At division the nucleus elongates, and the nucleolus stretches into a rod which appears like an axis in the nucleus, the chromosomes arranging themselves parallel to this axis. The substance of the nucleolar axis then gradually draws apart in the center and accumulates at the poles. The chromosomes distribute themselves in two groups, which gradually separate and gather around the two daughter nucleoli and the nucleus thus divides directly. In most cases there is no trace of a nuclear membrane around the nucleus at any period of its transformations.—B. M. DAVIS.

FARMER AND HILL¹³ have described the anatomy and development of *Angiopteris*, *Marattia*, and *Kaulfussia*. They find that the central cylinder of the stem in the first two genera originates as a solid tracheary rod sur-

¹³FARMER, J. BRETLAND and HILL, T. G., On the arrangement and structure of the vascular strands in *Angiopteris evecta* and some other Marattiaceae. *Ann. Botany* 16: 371-402. pls. 16-18. 1902.

rounded by phloem (protosteles). Ordinarily, after the exit of a number of monodesmi cleaf traces a mass of parenchyma makes its appearance in the center of the tracheary tissue, which the authors regard as a true pith or medulla. Gradually the "pith" becomes enlarged as the young stem grows stouter. Sieve tubes then make their appearance between it and the xylem. Later still an endodermis is formed within the tubular stele (siphonostele), but it is not clear from the author's description whether it originates in such a way as to leave their primary "pith" in continuity with the fundamental tissues of the true pith which finally shows itself within the fibrovascular zone. It seems probable from the course of development observed in similar instances that such is not the case. Sooner or later the fibrovascular ring becomes broken up into a zone of separate strands by the overlapping of the gaps which occur above the exit of the leaf traces. Subsequently the fibrovascular system is further complicated by the appearance of strands running through the pith and joining up the walls of the stelar tube just above the points of exit of the foliar traces. The increasing complexity of the commissures leads to the extremely involved condition of the fibrovascular system which is so characteristic of the adult marattiaceous stem. The authors were unable to investigate the ontogeny of a third genus, *Kaulfussia*, but concluded from the structure of the adult stem that the course of development of the strands is probably the same as in *Angiopteris* and *Marattia*.

They criticise the term *phloeoterma* proposed by Strasburger to denote the morphological boundary between the fibrovascular and fundamental tissues, and point out with great force the fallacy of admitting the phloeotermal value of the endodermal layer which surrounds $n+1$ fibrovascular strands, and denying it where the endodermal zone surrounds only one such strand. They conclude that the endodermis has no morphological value as a stelar boundary, both on account of its inconstant occurrence and of the frequent seriation of its cells with elements inside or outside the central cylinder. They consider that the tracheary tissue is the only reliable basis for morphological hypotheses, apparently losing sight of the fact that not unfrequently even the tracheary elements themselves appear in seriation with endodermal cells, and consequently, in accordance with the cell wall reticulum hypothesis, might belong outside the stelar system. It appears probable that greater clarity of view will supervene in developmental studies when with Sachs we cease to regard the cell wall reticulum as having any greater importance than an indication of the direction of the forces of growth. The morphological value of a structural feature seems rather to depend on its presence in older groups and in the young individual of higher groups, etc., than on histogenetic details which are extremely unstable in both animals and plants. Inconstancy of occurrence appears further to afford an argument rather for than against the ancestral character of any given morphological feature. It may consequently result that Strasburger's conception of a phloeoterma marking the boundary between the stelar and fundamental tissues will ultimately be

retained in a modified form, when the present extreme revulsion of the English school of anatomists from the epoch-making anatomical hypotheses of Van Tieghem has reached a condition of equilibrium.

The present work has resulted in the discovery of cambial activity in the parenchyma between the phloem and xylem of bundles in the young stem, which brings about the addition of fresh elements to the xylem. The authors discuss the parallel first instituted by Mettenius between the root-traversed cortex of the marattiaceous stem and the somewhat similar tissue present in the fossil genus *Psaronius*. They conclude that the two are not really comparable and suggest that in *Psaronius* the tissue in question results from the fusion of roots which are already outside the stem.—E. C. JEFFREY.

A NEW METHOD of studying the irritability of plant protoplasm has been devised and quite extensively applied by Bose¹⁴. It depends upon the existence of electric responses due to stimulation. As in animal muscle and nerve, if a limited portion of a plant tissue be injured in any way, there is produced a difference of electrical potential between the injured and the uninjured part, and a "current of injury" results, the injured region being positive with reference to the remainder of the tissue. In the case of animals a stimulus applied to a tissue exhibiting this current of injury causes a momentary but well-marked diminution in the current. A current of response or "action current" is produced which flows from the more active (uninjured) portion to the less active (injured) portion, thus producing a depression in the preexisting current of injury. This phenomenon, known in animal physiology as "negative variation," is found by Bose to occur quite generally in plant tissues. Stems, leaf stalks, flower stalks, and roots of various plants were used in the experiments. To produce the current of injury a slight burn with a potash solution is sufficient. For the negative variation a sharp mechanical blow upon the tissue or a slight torsion about its long axis was used. Records of the response were taken in the form of curve tracings, partly made by hand upon a revolving drum following the migrations of a beam of light reflected from the galvanometer, and partly recorded automatically by this beam upon a sensitive photographic plate. The response is found to be determined quantitatively by the intensity of the stimulus producing it, but some tissues (*e. g.*, leaf-stalk of turnip, celery, cauliflower) show fatigue if a uniform stimulus is repeated too often, and some show the so-called "stair-case effect" known for certain animal tissues.

Another and better method for investigating these phenomena obviates injury. The tissue to be tested is fixed firmly at a point between the two electrodes and a stimulus is applied on one side of the block thus produced. This stimulus (a blow or a torsion) is of course thus confined to the portion of the tissue on its own side of the blocking clamp, and a current of response

¹⁴BOSE, J. C., Electric response in ordinary plants under mechanical stimulus. *Jour. Linn. Soc. Bot.* 35: 275-304. *figs.* 25. 1902.

is exhibited, the stimulated portion being positive with reference to the other.

Several curious and apparently very important analogies between the electric responses in plant tissues and corresponding ones in those of animals were brought out. (1) In stale nerve the current of response is the reverse of what it is in fresh; it flows from the less excited to the more excited, but with very strong stimulation the response becomes again like that in the fresh material. Exactly the same phenomena are observed in plant tissues. (2) Decrease in temperature causes decrease in response in animals. In plants this is also true where the tissue is otherwise known to be easily affected by cold. But in hardy plants a lowering of temperature, unless it nears the death point, does not have much effect. (3) High temperatures nearing the death point produce a fall in the intensity of response in both animals and plants. This electric method furnishes an immediate and direct means of determining the death point, for here and beyond no response can be obtained. (4) Anaesthetics and poisons have the same effect on the electric response in plants as in animals. With the application of the reagent the response is gradually depressed until it finally ceases altogether. (5) In some cases of poisons where a large dose produces depression and annihilation of response, a small dose acts as a stimulating agent and produces a rise in the response curve. This is also known in some animal tissues.

These results seem to be almost a proof of the underlying identity, or at least remarkable similarity, of plant and animal protoplasm, and hence are to be regarded as exceedingly important and fundamental. I cannot resist the temptation to suggest here, in view of the long-continued discussions as to the point where life gives place to death, that we have perhaps in this electric response the best criterion yet discovered for determining when a tissue is alive and when dead. An arbitrary definition of life might be an aid in some cases, and probably the best one which can be framed (if the properties here described are shown to be general) is that protoplasm is alive when it exhibits electric currents of response.—BURTON E. LIVINGSTON.

RECENT STUDIES UPON REGENERATION: T. H. MORGAN (Columbia Univ. Biol. Series VIII. The Macmillan Co., N. Y. 1901) has published a volume dealing with regeneration in general, especially in animals. Chapter four is devoted to regeneration in plants, and the familiar work of Vöchting and Goebel is cited, though practically nothing that is new is introduced. Morgan holds, as do most authors, that in plants a latent bud develops, while in animals there is a restoration at the cut surface. He does not accept Goebel's idea that this is due to the fact that plants have latent buds and hence do not have to restore the lost part as do animals. He opposes Sachs' theory of "Stoff und Form," as well as Goebel's modification of this theory; buds do not remain latent because poorly fed, nor do they grow because they are well fed. Morgan fails entirely to accept natural selection as a cause for the development of the capacity to regenerate; organs which are not subject to

injury often regenerate, and organs of no value often replace valuable organs that were lost. Natural selection, he thinks, could not at once cause a lost organ to be perfectly restored, yet only a perfect restoration would be of any value. Teleological and vitalistic viewpoints are not looked upon with especial favor.

K. GOEBEL (*Biol. Centrabl.* 22:385-397, 417-438, 481-505, 1902) has been stimulated by the recent work of Morgan and Driesch to present the present condition of our knowledge concerning regeneration in plants. He cites certain ferns in which regeneration occurs in the normal life history, while there are other cases in which a stimulus is necessary; the former live in moist, the latter in dry situations. In *Bryophyllum* the latent leaf buds commonly develop only when the leaf has fallen to the ground; if the midrib be cut, they develop while still on the parent plant. So too the removal of the stem buds causes the leaf buds to develop. Goebel thus thinks that there is a correlation between the stem and leaf buds, the latter being normally inhibited from lack of food. If all leaf buds are removed, new primordia (*Anlagen*) appear at the leaf base. Other plants in which leaf buds occur are cited. Goebel has also worked on young plants of *Cyclamen*, a genus which was shown by F. Hildebrand in 1898 to have remarkable powers of regeneration. Hildebrand found that if the blade of the first leaf were removed, a kidney-shaped wing, resembling the lost leaf, was regenerated on each side of the petiole, and at the cut surface. If part of the blade is cut it is restored much as in animals; if the cut is made down on the petiole, the regenerated leaves may have stalks. If the young tuber is cut, leaves develop around the cut edge. An interesting summary is given of botanical literature dealing with regeneration.

Other papers on regeneration may be briefly noted: E. HEINRICHER, also J. PALISA (*Ber. Deutsch. Bot. Gesell.* 18:109-121, 398-410. 1900) have studied regeneration in *Cystopteris*. Palisa found that any epidermal cell in the bulbil leaves can regenerate a bud capable of becoming a new plant. H. WINKLER (*Jahrb. Wiss. Bot.* 35:447-469. 1900) has studied *Bryopsis*, which years ago Noll found to display a reversal of polarity. Noll ascribed this to the influence of gravity, but Winkler has shown that light is the determining factor. He suggests that the best nourished parts regenerate stems and the most poorly nourished parts rhizoids; the migration of chloroplasts toward the light may thus be the decisive factor in the case. Winkler regards the development of rhizoids at the stem pole as a case of heteromorphosis—the first noted in plants. This author also holds that a number of plants regenerate from the cut surface, rather than from buds, exactly as in animals.—F. NOLL (*Ber. Deutsch. Bot. Gesell.* 18:444-451. 1900) accepts Winkler's view that light is the leading factor, but thinks that heteromorphosis has been known in plants though not distinctly claimed.—H. WINKLER (*Ber. Deutsch. Bot. Gesell.* 20:81-87. 1902), as well as Hildebrand and Goebel,

has been studying *Cyclamen*. Among his important results, we may note that the place at which regeneration occurs may be altered by putting a plaster of Paris cap over the cut end of the petiole. A similar cap or a coat of shellac over the leaf causes regeneration without cutting. —S. PROWAZEK (Biol. Centralbl. 21:87-95, 144-155. 1901) and O. HÜBNER (Zool. Jahrb. 15:461-498. 1902) have studied regeneration, chiefly in animals, though working on a few plant forms. Hübner adheres to Weismann's adaptation theory and thinks that the capacity for regeneration has been developed by natural selection.—H. C. COWLES.

SOME RECENT BULLETINS of the United States Bureau of Forestry add to the knowledge of the silvicultural (ecological) behavior of certain trees. Olmsted¹⁵ discusses the relation of three forest societies in Arkansas. The "pine ridges" are the most xerophytic. More than 50 per cent. of the ridges have pine, 38 per cent. being short-leaf pine (*Pinus echinata* Mull.) and 16 per cent. loblolly pine (*Pinus taeda* Linn.). The remaining portion comprises oaks and other deciduous trees. Seedlings of the pines mentioned are found not to be tolerant of shade. In more mesophytic conditions, on the "pine flats," the loblolly pine comprises 34 per cent. of the growth, and the short-leaf pine only 20 per cent., the remaining being deciduous trees. In the hydro-mesophytic conditions along streams, the so-called "hardwood bottoms," the pines are entirely absent. This is due to the fact that these lands are frequently flooded, also the ground is too heavily forested for the germination of pine seedlings. The author gives silvicultural notes on the most important species, and in part two discusses the management of the forest.

In another bulletin Allen¹⁶ shows that the western hemlock (*Tsuga heterophylla* Sargent) requires a climate with a heavy rainfall, and that it is exceedingly tolerant of shade. This latter characteristic is of very great importance in determining the composition of the forest in which it grows. The author also gives an excellent report of the insects that infest the tree, and emphasizes the fact that its usefulness as a lumber, tanning, and paper pulp tree has been greatly underestimated.—H. N. WHITFORD.

¹⁵OLMSTED, F. E., A working plan for forest lands near Pine bluff, Arkansas. Bureau For. U. S. Dept. Agric. Bull. 32. pp. 48. pls. 11. figs. 9. 1902.

¹⁶ALLEN, E. T., The western hemlock. Bureau For. U. S. Dept. Agric. Bull. 33. pp. 55. pls. 12. 1902.

NEWS.

DR. H. O. JUEL has been promoted from a docentship to a professorship in the University of Upsala.

THE LAMARCK HERBARIUM has been secured by the French government and deposited at the Jardin des Plantes.

M. A. HOWE, of the New York Botanical Garden, is engaged in a survey of the algal flora of the Florida Keys.

PROFESSOR WLADISLAW ROTHERT, of Charkow, has been elected professor of botany in the University of Odessa.—SCIENCE.

DR. ADRIEN LEMAIRE, well known for his works on diatoms, on the anatomy of roots, etc., died at Nancy, October 23, 1902.

DR. J. B. DETONI has been appointed Professor of Botany and Director of the Botanic Gardens at the University of Modena, to succeed the late Professor Antonio Mori.

F. S. EARLE, of the New York Botanical Garden, is in Jamaica, in company with William Fawcett, investigating the diseases of logwood, banana, cocoanut, ginger, and pineapple.

THE SECOND VOLUME of Coulter and Chamberlain's *Morphology of Spermatophytes*, entitled *Morphology of Angiosperms*, is in the hands of the publishers, D. Appleton and Company.

PEARSON'S COLLECTIONS of Hepaticae have been secured by the National Herbarium at the British Museum. It contains about 9,000 specimens, among which are many types and the material used in preparing several well-known papers.

ERNST A. BESSEY, explorer of the U. S. Department of Agriculture, has returned from his journey into Turkestan, and has entered the University of Halle for further botanical study. The easternmost point reached by him was Andijan, in the province of Ferghana.—SCIENCE.

THE CAMBRIDGE UNIVERSITY Press will shortly publish the first volume, containing the introduction, the gymnosperms, and the monocotyledons, of a new introduction to systematic botany by Dr. Rendle. The work, which is entitled "A systematic account of the seed-plants," is to be in two volumes and will be fully illustrated.—JOUR. BOT.

THE FIRST number of a new mycological journal, entitled "Annales Mycologici" and edited by Professor H. Sydow of Berlin, will appear in January 1903. The closing statement of the announcement is as follows:

"It will be seen from the foregoing that the *Annales Mycologici* are destined to supply a long-felt want. In fact every mycologist will not be able to get on without them, nor will any botanical museum be able to possess an up-to-date library without taking in the new periodical."

KIICHI MIYAKE (Ph. D. Cornell 1902) has recently received an appointment from the government of Formosa for two years travel and study in Europe. Dr. Miyake is a graduate of the Doshisha College in Japan, afterward spending four years at the Tokyo Imperial University, after which he entered Cornell University in September 1899, where he has spent two years in continuing his graduate work, giving especial attention to fertilization and embryology in the Phycomycetes and in the Abietinae.

POSTELSIA, the yearbook of the Minnesota seaside station, has appeared, containing the following papers for 1901: Uses of marine algae in Japan, by K. YENDO; Remarks on the distribution of plants in Colorado, east of the divide, by FRANCIS RAMALEY; The phylogeny of the cotyledon, by HAROLD L. LYON; Botanizing in Jamaica, by ELOISE BUTLER; Algae collecting in the Hawaiian islands, by JOSEPHINE E. TILDEN; The distribution of marine algae in Japan, by K. Yendo; The kelps of Juan de Fuca, by CONWAY MACMILLAN.

FROM THE *New Phytologist* we learn the following facts in reference to some of the more important botanical papers read at the Belfast meeting of the British Association, in addition to those recorded in BOT. GAZ. 34: 320. 1902. Z. C. BOSE showed his experiments on the electrical response of plant tissues to mechanical stimulation; A. MACFAYDEN gave an account of the researches conducted by him and S. ROWLAND on the suspension of life at low temperatures; H. H. DIXON gave an account of some experiments on the resistance of seeds to high temperatures; MISS MATTHÆI presented a paper on the effect of temperature on carbon dioxide assimilation; F. W. OLIVER gave a preliminary account of an investigation of *Torreya* being made by him and MISS EDITH CHICK; MISS MARGARET BENSON spoke of the seed-like fructifications of *Miadesmia* (Lycopodiales), and of a group of sporangia that may be the first known example of a spore-producing member of the Cycadofilices; L. PRAEGER read a paper on the composition of the flora of northeastern Ireland. We have already noted (BOT. GAZ. 34: 320. 1902) the papers of J. Reynolds Green (the president), A. C. Seward and Sybille Ford, J. C. Willis, Harold Wager, H. Wright, and Messrs. Seward and Arber.

GENERAL INDEX.

The most important classified entries will be found under Contributors, Hosts, Personals, and Reviews. New names and names of new genera, species, and varieties are printed in **bold-face type**; synonyms in *italics*.

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